

FUNCTIONAL MORPHOLOGY AND FLIGHT KINEMATICS OF
Artibeus jamaicensis (CHIROPTERA, PHYLLOSTOMIDAE)

By

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by

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Abstract of Dissertation Presented to the Graduate School
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FUNCTIONAL MORPHOLOGY AND FLIGHT KINEMATICS OF
Artibeus jamaicensis (CHIROPTERA, PHYLLOSTOMIDAE)

By

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The functional morphology of the pectoral girdle and arm of Artibeus jamaicensis (Chiroptera, Phyllostomidae) is interpreted on the basis of gross dissection and electromyographical analysis (EMG). Electromyographic data obtained during flight for 15 muscles elucidate several temporal patterns of activity associated with the wingbeat cycle that are not similar to the patterns of flexor, extensor, and bifunctional muscles observed in terrestrial mammals. Abductor muscles exhibit intense activity associated with the early upstroke phase of the wingbeat cycle and include clavotrapezius, acromiotrapezius, latissimus dorsi, teres major, acromiodeltoideus, spinodeltoideus, and triceps brachii (long and lateral heads). All abductors except for the triceps brachii exhibit a secondary period of low-amplitude activity associated with the early downstroke. Adductor muscles exhibit primary activity immediately prior to and during the early downstroke phase. The adductors include serratus ventralis thoracis, pectoralis, and

clavodeltoideus. Bifunctional muscles exhibit a single period of activity through most of the wingbeat cycle, or two separate periods of high-amplitude activity during a wingbeat cycle. The bifunctional muscles include spinotrapezius, supraspinatus, infraspinatus, and subscapularis. Dissection of all other muscles of the shoulder and antebrachium form the basis of interpreting musculoskeletal movements during flight in Artibeus. The major muscles of support in Artibeus include serratus ventralis thoracis, pectoralis, and the trapezius group. These muscles support the trunk between the wings during flight or terrestrial locomotion. Propulsion during flight differs from that observed during stepping in terrestrial mammals. During the wingbeat, pectoralis provides the major component of thrust, both by adducting and pronating the wing. Although latissimus dorsi is a major propulsive muscle during stepping in terrestrial mammals, its major function in Artibeus is to abduct the wing and reposition the wing prior to the beginning of a downstroke.

INTRODUCTION

Bat flight is energetically expensive (Thomas and Suthers, 1972; Carpenter, 1975; Thomas, 1975, 1981) and requires extensive alterations of the generalized mammalian morphology (Miller, 1907; Vaughan, 1970a). In order to understand how bats fly, one must both study their anatomy as well as the subtle interactions between the nervous and muscular systems of several bats must be studied. This study provides information about the neuromuscular and osteological mechanisms associated with flight in a frugivorous bat, Artibeus jamaicensis (Microchiroptera, Phyllostomidae). The objectives of the project are to describe in detail the musculoskeletal system of Artibeus, to illustrate the kinematics of the normal wingbeat cycle, and to obtain electromyograms during flight for the major muscles of the shoulder region and arm.

Three factors make Artibeus jamaicensis desirable for morphological analysis. First, Artibeus is a ubiquitous neotropical bat whose basic biology has been well documented. The available information regarding the foraging and flight habits of this bat permits deduction of the demands placed on the bat. Second, Artibeus

jamaicensis is easily maintained in captivity during the duration of an experimental period (Rasweiler, 1977). Third, Artibeus is placed in the family Phyllostomidae (Jones and Carter, 1976), a family that has not been employed in previous EMG studies.

The diet of Artibeus includes fruits, flower products, and leaves (Goodwin and Greenhall, 1961; Villa-R., 1967; Heithaus et al., 1975; Gardner, 1977; Bonaccorso, 1979). Insectivory is insignificant in this species even though Tuttle (1968) observed Artibeus jamaicensis in Mexico feeding on blackflies within a cave. The bats usually transport relatively heavy fruits from their source to adjacent feeding roosts except when too large to carry efficiently (Morrison, 1978a; Bonaccorso, 1979). Thus the wings of Artibeus need to be capable of producing lift at low speeds without a great deal of maneuverability.

The flight style of Artibeus differs from that of Desmodus, Antrozous, and Myotis, three bats previously studied with electromyography. The vampire, Desmodus, is characterized by its direct, swift flight (Altenbach, 1979). Antrozous and Myotis are both insectivores but each employs slightly different foraging behaviors. Antrozous is a long-eared bat and either gleans insects from foliage or preys upon large, slow-moving insect species at low altitudes. Myotis myotis tends to also be an opportunistic gleaner, searching for and obtaining insects from the surface of foliage or the ground (Findley, 1972). Desmodus, Antrozous, and Myotis all forage for extended

periods of time during the night. Antrozous was reported to engage in continuous foraging on the wing for one to four hours during early evening and later for several hours before dawn (O'Shea and Vaughan, 1977). Myotis lucifugus similarly feeds for several hours during early evening, and again for several shorter periods before dawn (Anthony and Kunz, 1977). I expect behavioral studies will show Myotis myotis has a similar time-energy budget. Turner (1975) reported that Desmodus spends one to three hours foraging per night and found that the bats spent a mean of one hour per night searching for their prey. Artibeus, in contrast, tends to spend relatively little time in flight during the night (Morrison, 1978a; 1978b). Artibeus also is not very maneuverable and is easily captured in nets. There are two brief flights between the day roost and the food source: one at dusk to the food and one shortly before sunrise back to the day roost (Morrison, 1978a). Morrison found that day roosts were never very distant from a source of ripe fruit. At night, Artibeus selects fruit at the source tree and then carries the fruit to an adjacent feeding roost, often in another tree or in a cave (Dalquest, 1953; Morrison, 1978a; Bonaccorso, 1979). After chewing the fruit and swallowing juice and edible parts, the bat ejects the remaining fruit pulp and seeds before returning to the source tree for another fruit. These feeding flights are repeated many times during the night.

Artibeus jamaicensis transports fruit on average 270 m from the parental trees to feeding roosts (Janzen et al., 1976).

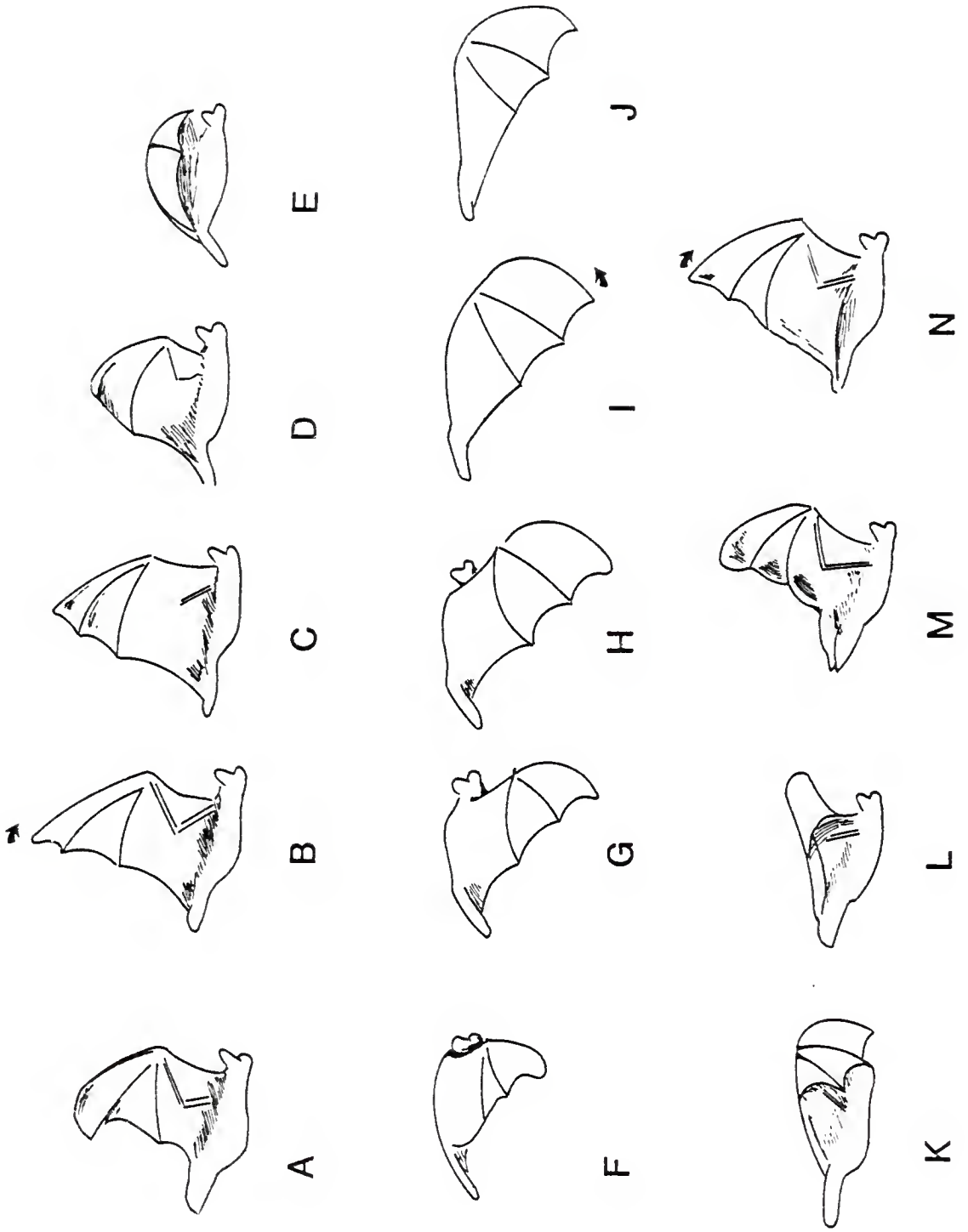
Morrison (1978a) observed that the distance between several Ficus insipida and Ficus yaponensis, two species of figs important as food trees, and the adjacent feeding roosts ranged from 25-400 m (mean 175 m). It is not clear why these bats carry fruits away from the parent tree. Janzen et al. (1976) speculated that branch morphology and odor in Andira inermis evolved to insure dispersal of the seeds away from the parent tree. Seed mortality resulting from fungal infections and weevil predation was most severe beneath the parent trees but declined with distance away from the tree. They were unable to demonstrate a clear cause and effect relationship, but did speculate that bats were intolerant of the odor associated with many ripe Andira fruit. As an alternative hypothesis, several authors suggested that Artibeus carried fruit to a distinct feeding roost to decrease predation (Fenton and Fleming, 1976; Morrison, 1978a; August, 1979). Artibeus avoid visually orienting predators such as owls and opossums, by feeding only on dark nights or during dark periods of the night (Morrison, 1978b). Specific cases of predation by Didelphis marsupialis upon Artibeus were reported in Venezuela (August, 1979). In any case, Artibeus make a number of short flights during the night to and from a ripe fruit tree.

The neuromuscular control of flight can be correlated with similar mechanisms in operation in the control of terrestrial locomotion. Analysis of terrestrial involved resolution of the locomotor activity of each limb into successive strides or step cycles, and quantification

of the interaction of these events between the limbs (gait analysis) (Wetzel and Stuart, 1976). Philippson (1905) described four stages in the step cycle of dogs, beginning with foot liftoff: F or flexion phase is when most joint angles in the limbs decrease; E1 is the final portion of the "swing" or non-support phase of the stride; E2 is the first portion of the "stance" or support phase and includes some passive joint flexion as a result of the limbs yielding under the animal's weight; E3 is the final portion of the "stance" phase during which all joints are actively being extended and maximum thrust is being generated by the limb. Neurophysiologists studying vertebrate locomotion have long focused on events surrounding the two reversal points in the stride. For example, Sherrington (1910) made the observation that a graded alternation of activities occurred in the flexor and extensor muscles and that this alternation could be invoked in a model of reflexive control of the step cycle (cf. Wetzel and Stuart, 1976).

As an analogy, Hermanson and Altenbach (1981) expressed the chiropteran wingbeat cycle as being a quantifiable and repeated unit of normal bat flight. Individual wingbeats exhibit little variation among conspecific individuals performing the same locomotory tasks under similar conditions. The chiropteran downstroke, or adductor phase, is similar in basic form and timing to the E2-E3 phases of the Philippson step cycle and produces components of both lift and thrust (Norberg, 1976). The chiropteran upstroke, or abductor phase, parallels the F-E1

Figure 1.--The wingbeat cycle of Artibeus jamaicensis. Each image was traced from a 16 mm movie film. About 8 msec elapsed between each image. The downstroke begins with frame B, and ends at frame H. Upstroke movements begin during frame I and continue through frame M. The flick phase, not shown, occurs rapidly during the interval between frames L and M when the wing is rapidly pronated.



phases of overground locomotion in its function as a recovery stroke. The last portion of the upstroke often includes a thrust-producing "flick phase" (Norberg, 1970, 1976). Except for the flick phase, it is not practical to subdivide the upstroke or downstroke because of the smooth arc followed by the wing during each phase (Figure 1).

Engberg and Lundberg (1969) demonstrated that cat limb muscles exhibit characteristic activity profiles during overground locomotion: extensor or flexor muscles produce a cumulative effect on the skeletal system through overlap or coactivation, and muscles that span two joints produce a complex function including both flexion and extension. Engberg and Lundberg reported extensor activity prior to foot touchdown during normal stepping. This important observation indicated that muscle activity could be preprogrammed at the spinal or supraspinal level, taking precedence over reflexive control of the step cycle (Wetzel and Stuart, 1976). Subsequent studies demonstrated that the EMG profiles for homologous mammals are conservative among mammals, with subtle differences in timing related to differing functional demands being placed upon the musculoskeletal system in various species (English, 1978a, 1978b; Gambaryan, 1974; Rasmussen et al., 1978; Tokuriki, 1973a, 1973b).

Hermanson and Altenbach (1981, 1983) assembled EMG data for muscle activity during flight in an insectivorous bat, Antrozous pallidus (Vespertilionidae). Of 17 muscles studied, 11 muscles demonstrated patterns of either adductor or abductor activity. Only six muscles

exhibited a complex bifunctional pattern of activity. The adductor muscles demonstrated an onset of activity on average 15-25 msec prior to initiation of the downstroke. This pattern is similar to the El extensor coactivation observed prior to foot touchdown in cats (Engberg and Lundberg, 1969) and suggests that similar neural control mechanisms are involved in regulating both the terrestrial step cycle and the aerial wingbeat cycle. Despite gross anatomical modification during the evolution of the chiropteral musculoskeletal system, the patterns of limb movement and muscle activity remained relatively unchanged from the basic mammalian condition.

This study presents the descriptive anatomy of the locomotor system of A. jamaicensis, including the shoulder girdle, arm, and forelimb portions of the wing. Descriptions are accompanied by functional hypotheses for each muscle following a format employed in a number of studies on the mammalian musculoskeletal system (Howell, 1926; Rinker, 1954; Klingener, 1964; Woods, 1972). Additionally, EMG data are presented for 15 of the 17 muscles that were previously analyzed in Antrozous pallidus (Hermanson and Altenbach, 1983). These data are compared with simialr EMG observations upon terrestrial mammals.

MATERIALS AND METHODS

Ten skeletons and ten alcoholic specimens of Artibeus jamaicensis were used for descriptive study. Dissection specimens were preserved in a solution of 10 percent solution of formalin for 10-14 days and were later stored in 70 percent ethanol or 40 percent isopropanol. Complete dissections performed on the shoulder, arm, and antebrachial regions form the basis of descriptions and illustrations presented in this study and for the design of electromyography experiments.

Terminology used in my study conforms to recommendations by the International Commission on Veterinary Anatomical Nomenclature (Nomina Anatomica Veterinaria, 1975). Although this procedure initially appears to pose difficulty in making comparisons with previous studies on chiropteran morphology, relatively few new terms are introduced. Strict adherence to the terminology of the Nomina Anatomica Veterinaria (NAV) will provide a consistent vocabulary for effective communication about the subject and will facilitate communication with researchers who have not mastered the specialized jargon of bat anatomy.

Several terms are used throughout this text to indicate direction along the body axis or direction of movement at a joint. The terms

cranial and caudal have replaced anterior and posterior, respectively, in all cases where the latter terms have been used in the chiropteran literature. Cranial refers to the cranial end of the animal, or indicates that a structure passes from a point on the body along a line towards the transverse plane of the head. Caudal indicates the opposite direction to cranial: to or towards a transverse plane containing the caudal vertebrae. Medial and lateral are used to indicate position or movement towards or away from the medial plane of the body. Flexion and extension refer to a decrease or increase, respectively, in the angle between two bones. Adduction is used to denote movements of the wings, humerus, or clavicle towards the medial plane on the ventral surface of the body. Abduction of the wings, humerus, or clavicle is a movement away from the median plane of the ventral surface of the body. Rotation of a bone about its long axis is described as supination, or outward rotation of the top or lateral surface of the bone, and pronation, an inward rotation of the top or lateral surface of the bone. To facilitate comparison with terrestrial mammals, the arm and antebrachium are described in the position of maximal adduction. Thus these bones have cranial, caudal, lateral, and medial aspects. The carpus and digits are described as if they are held horizontally at the side of the body. These elements have cranial, caudal, dorsal, and ventral (palmar) aspects. The apparent inconsistency in terms and orientation between the anatomical position of the arm and carpus is in fact the traditional and accepted format for descriptive purposes.

Skeletons were measured with dial calipers in order to describe shape and size of individual bones. This information is useful in estimating position or attachments of soft tissues with respect to the skeleton.

Muscle origins and insertions were described relative to named structures or surfaces of individual bones: the extent of muscle attachment to long bones is expressed as a percentage or proportion of the total length of the bones. Fiber orientation was expressed with respect to the long axis of a muscle, along a line fit by eye between the lines of attachment.

Synchronized film and EMG records were obtained with a system initially described in Altenbach (1972, 1979) and modified by Hermanson and Altenbach (1981). A Hycam high-speed cine camera (Red Lakes Laboratories, Inc.) photographed flight sequences at film speeds of 300-400 frames per second. Myopotentials were recorded from a bipolar fine copper wire electrode implanted in the muscle belly. Implantation was achieved by a simple microsurgical procedure. An incision was first made in the dorsal integument superficial to the lumbar region and a silicone plug assembly was sutured to the muscle and ligaments of the paravertebral region. Electrodes were passed subcutaneously to a second incision at the level of the specific muscle being studied. A shielded cable surrounding the electrode assembly served as a tissue ground. With the aid of a microscope, the electrode tips were inspected to insure that less than

0.5 mm of the tip was bared. The tips were then placed in the muscle belly with a 27 guage hypodermic needle, and both incisions were sutured shut with 6-0 Ethicon nylon suture. Methoxyfluorane was used as a short term anesthetic agent with excellent results. Data were recorded shortly after the bat exhibited normal locomotor behavior and within three hours of surgery. Extended delays between the time of implantation and recording sessions resulted in less than satisfactory results, apparently as a result of toxic reactions between the copper electrode material and adjacent tissues. Inspection of one implantation that had been in place for 24 hours showed significant tissue necrosis in the muscle for a 2 mm diameter around the electrode tip. Only one muscle was studied per experiment. Each implant was visually inspected at the conclusion of each recording session to verify that the electrode remained in place. Each animal was allowed to recover for at least one week before being used in further experiments.

Normal flight was studied with single frame analysis of films of normal horizontal flight sequences. Single film frame images were projected with an L and W motion analyzer (Model 224A) and were traced to ascertain wingtip motion and joint position in the wing. Vertical displacement of the wingtips was used to determine the turnover points of adduction and abduction. The beginning of a downstroke was treated as the beginning of a wingbeat cycle and was assigned a numerical value of 0.000 (Figure 1, frame B). A complete wing cycle included values between 0.000 and 1.00, with 1.00 representing the final frame of an

upstroke (Figure 1, frame M). The transition between downstroke and upstroke (Figure 1, frame H) and periods of muscle activity are expressed as a mean percentage of a complete cycle.

Estimation of aerodynamic parameters was accomplished by measuring the dimensions of the wing and body of two fresh specimens of Artibeus jamaicensis. The mass of each bat was obtained to the nearest 0.5 g. Wing area was estimated by drawing the outline of the body and fully outstretched wing of each bat on paper. The cut-out outline of the airfoil was then weighed to the nearest 0.0005 g and then compared to the mass of a .100 m² square of the same paper to calculate actual wing area. Wingspan was measured along a line between the two wingtips. Aspect ratio is the ratio of length to width of the airfoil. The equation for aspect ratio is b^2/A (Norberg, 1981). Wingloading is the ratio of body weight to wing area, W/A (Norberg, 1981).

FLIGHT AND AERODYNAMICS

Results

The temporal relationship between the downstroke and upstroke is critical in the interpretation of EMG data. In part, this relationship reflects whether or not the activity of a given muscle is coincident with or occurs before or after a particular event, such as the beginning of a downstroke. During all filming sessions, flight was observed to detect any grossly abnormal flight behaviors. All flight sequences exhibiting turning behavior or altitude loss were eliminated from consideration. The wingbeat cycle of Artibeus appeared to be conservative during slow horizontal flight, based upon unaided visual observation as well as initial study of the film records. However, analysis of the film revealed slight differences in the flight of restrained and unrestrained animals.

During unrestrained flight in two bats, the downstroke encompassed 55.1 percent of the wingbeat. In contrast, bats that carried an electrode and plug assembly exhibited a mean downstroke of 49.44 percent. During unrestrained locomotion, the bats averaged 10.08 wingbeats per second. Records analyzed from four EMG experiments (clavotrapezius, spinotrapezius, clavodeltoideus, and infraspinatus) demonstrated a mean wingbeat frequency of 10.45 wingbeats per second.

Figure 2.--Wing and body movements during slow forward flight in *Artibeus jamaicensis*. The bat flew from left to right at 2.19 m/sec. The movements of the wingtip (), wrist (x), foot (o), and ear (.) were plotted during two wingbeats. The interval between each symbol was about 8.30 msec. There were two periods when the ear was obscured by the position of the wing during a wingbeat cycle.

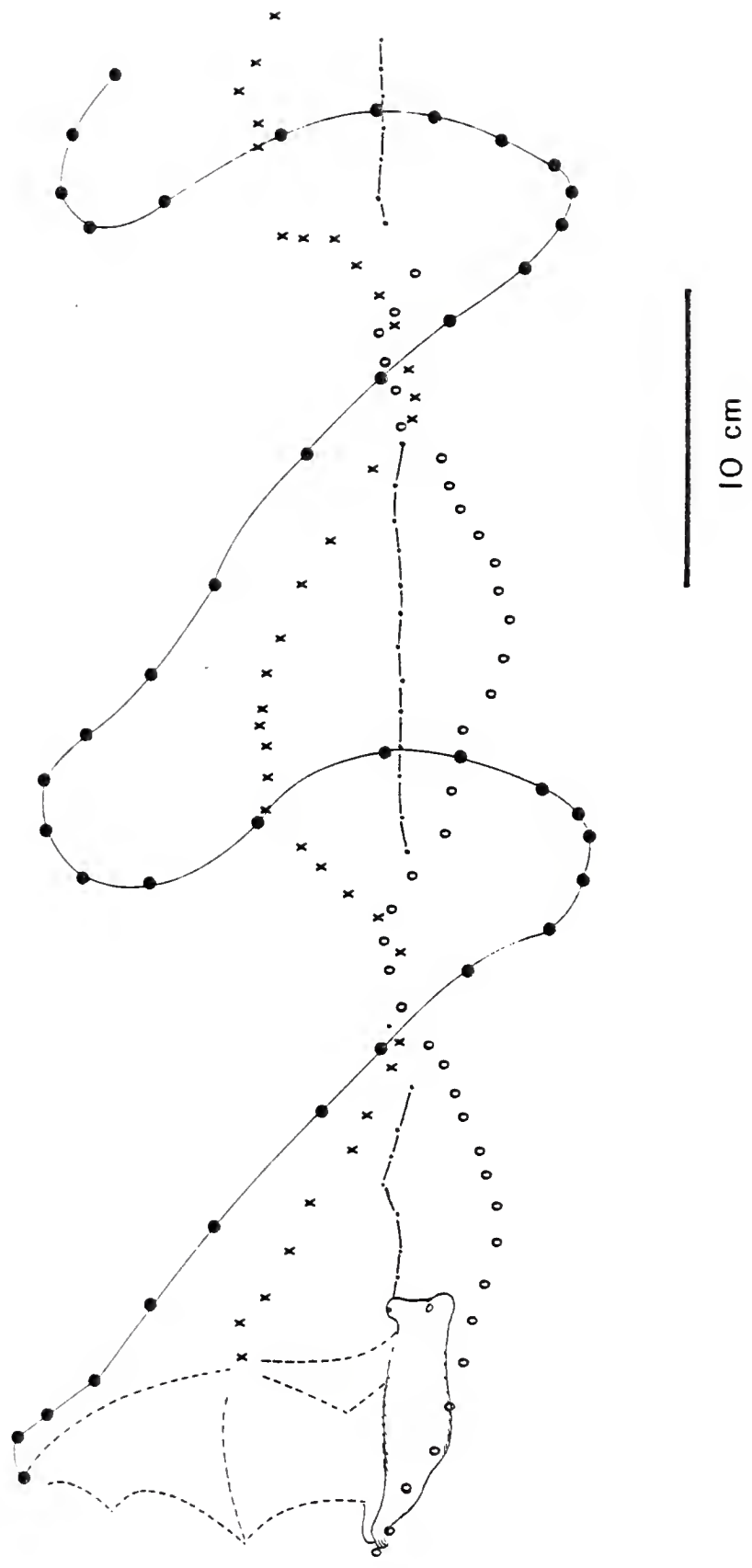


Figure 3.--Wing and body movements during slow forward flight in Artibeus jamaicensis. The bat flew from left to right at 2.85 m/sec. The movements of the wingtip (), wrist (x), foot (o), and ear (•) were plotted during two wingbeats. The interval between each symbol was approximately 5.10 msec.

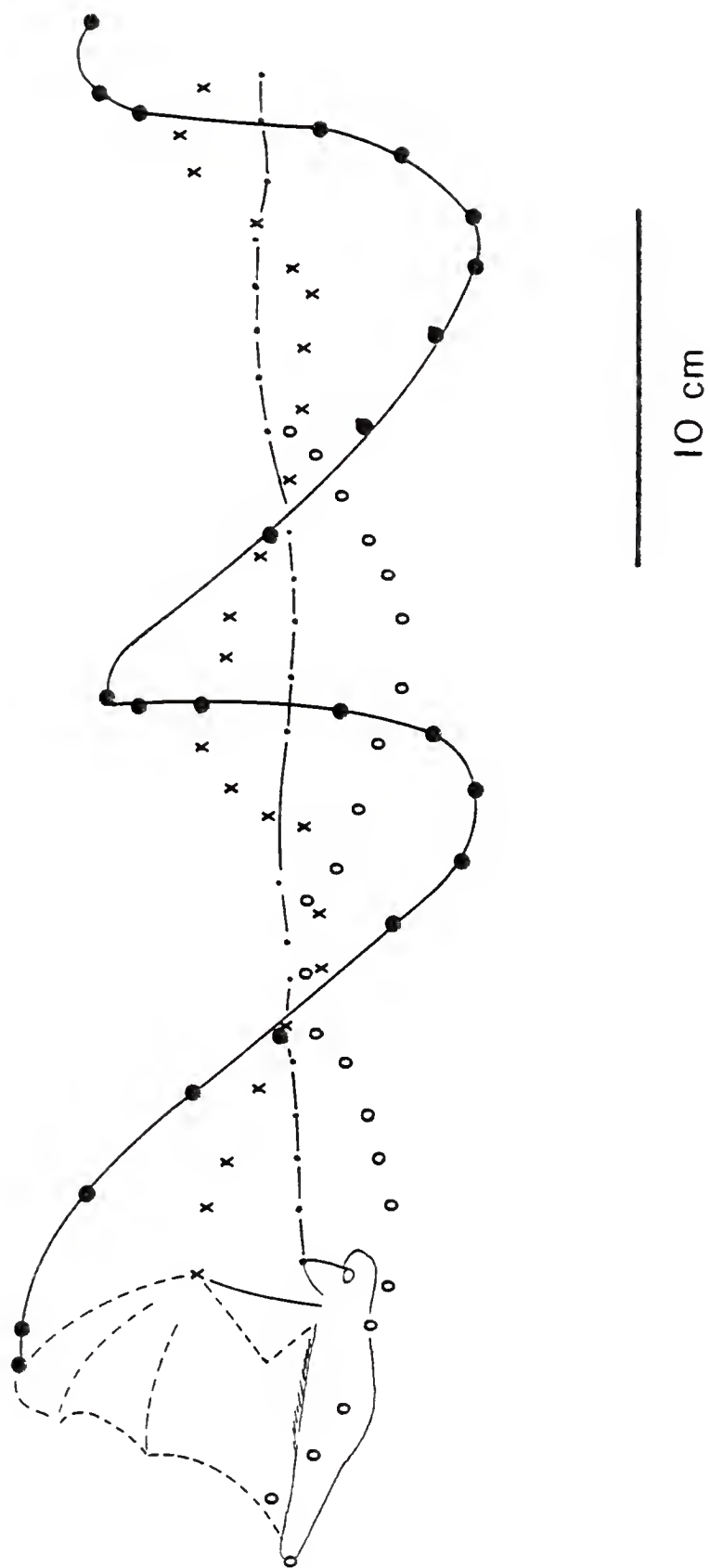


Figure 4.--Wing and body movements plotted relative to still air during slow forward flight in Artibeus jamaicensis. The bat flew from left to right at a velocity of 2.15 m/sec. (A) The movements of the wingtip are plotted relative to the body. (B) The movement of the wrist is plotted relative to the body.

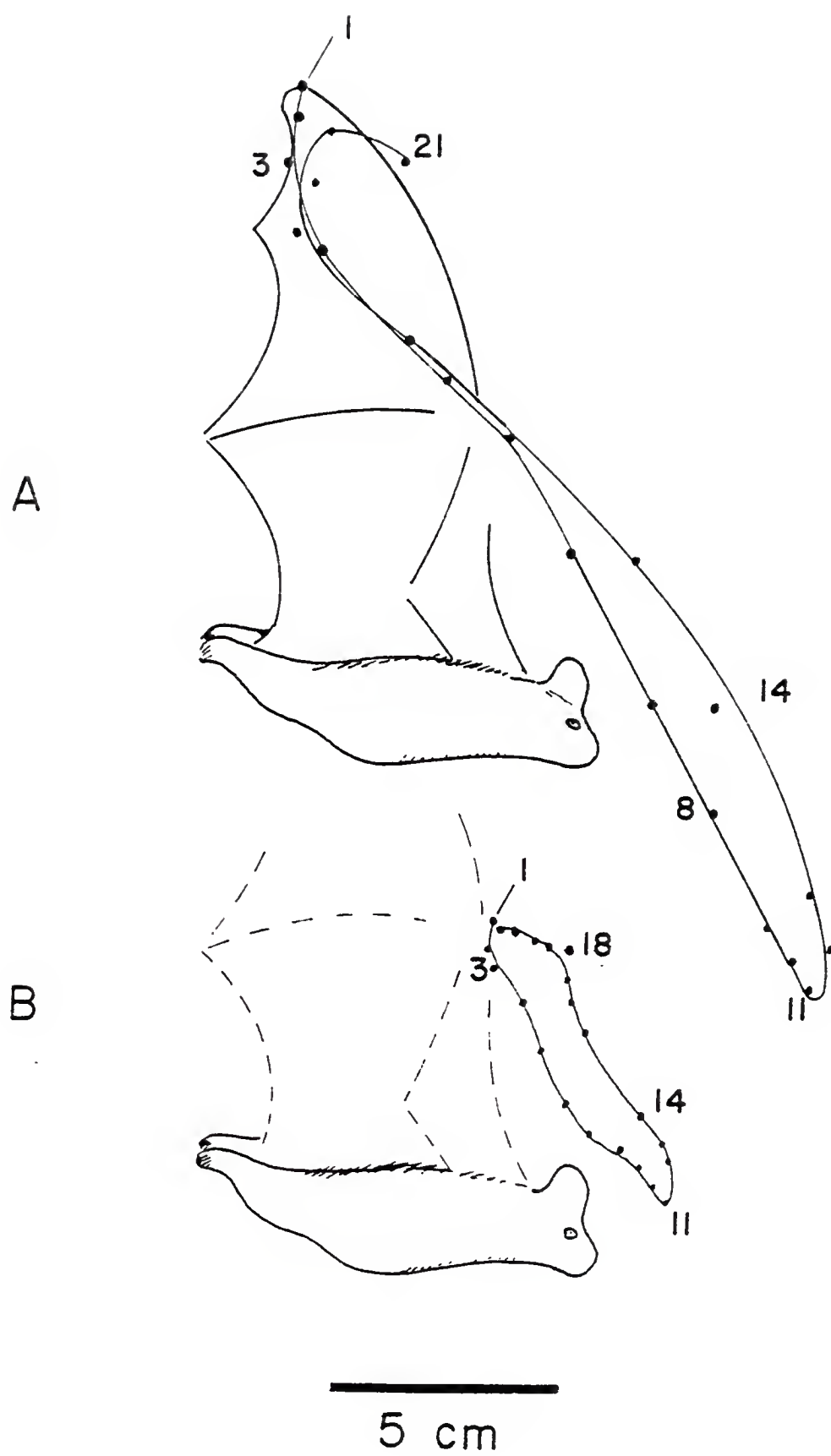


Table 1. Aerodynamic parameters of the wing in two fruit bats, Artibeus jamaicensis. All measurements are recorded in meter-kilogram-second units.

mass	0.04 kg	0.03 kg
weight	0.40 N	0.32 N
wing span (b)	0.39 m	0.32 m
wing area (A)	0.02 m ²	0.02 m ²
aspect ratio (b^2/A)	6.79	6.55
wing loading (W/A)	16.74 N/m ²	15.47 N/m ²

Analysis of one sequence of unrestrained flight is provided to illustrate airspeed and movement of several parts of the body and wing (Figures 2-4). Plots of head movement exhibited forward velocity ranging from 2.19-2.85 m/sec. At the beginning of the downstroke, the wingtip was positioned above and caudal to the center of the body. The wing was adducted, but moved with an initial caudal sweep of the wingtip relative to the center of the body. After approximately 15 msec, the adduction of the wingtip exhibited an increasing cranial component of movement. The wrist moved in synchrony with the wingtip but travelled through a smaller excursion. The wingtip continued moving ventrally and cranially through 62.5 percent of the wingbeat (Figure 2, Symbols 2-12). The wingtip and wrist synchronously showed abduction at the beginning of the upstroke. There was a cranial movement of both elements for approximately 5 msec. Subsequently, abduction of the wingtip and the wrist included a caudal component of movement for about 26 msec until the beginning of the flick phase. During the flick phase (Figure 2, Symbols 18-21) the outer portion of the chiropatagium was rapidly pronated. Cranial movement of the wingtip occurred during the flick phase, which lasted approximately 5 msec, or until the beginning of the downstroke. During the entire upstroke, movement of the wrist was in a dorsal and caudal direction. Thus, during the wingbeat cycle the wrist followed an elongated elliptical path. The path of the wingtip was best characterized as a tight and complex figure eight when viewed laterally.

Several measures are used in the description and comparison of the aerodynamic properties of Artibeus jamaicensis. Based on two specimens obtained in Haiti, the following means were obtained for these parameters: mean wing area, inclusive of the body, 0.02 m^2 ; wingspan, 0.38 m ; aspect ratio, 6.67 ; wingloading, 16.11 N/m^2 .

Discussion

The wing and flight characteristics of Artibeus jamaicensis are generalized in comparison to many other bats. Analysis of the flight kinematics and wingshape demonstrates that Artibeus is capable of slow flight in the forest canopy but not the faster, more maneuverable flight associated with the pursuit of insects among dense vegetation or in open airspace.

The data obtained during EMG experiments on Artibeus represent a departure from the mean downstroke times observed during the unrestrained flight sequences. These EMG flight data are comparable to downstroke phase relationships reported during EMG studies in Antrozous where a range of 39.7 to 52.3 percent was reported for the downstroke period (Hermanson and Altenbach, 1983). The downstroke of flying animals lasts longer than the accompanying upstroke (Aymar, 1935; Brown, 1963; Norberg, 1976; Brandon, 1979). Flying birds or bats can be seen to oscillate in a vertical plane during flight, losing a slight amount of altitude during each upstroke phase, and regaining altitude during the subsequent downstroke (Eisentraut, 1936). The upstroke does

not provide sufficient lift to counteract the effect of gravity except in certain species that employ a hovering mode of flight (Norberg, 1975).

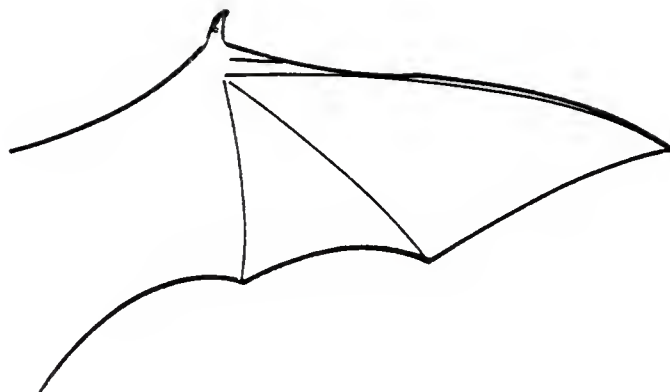
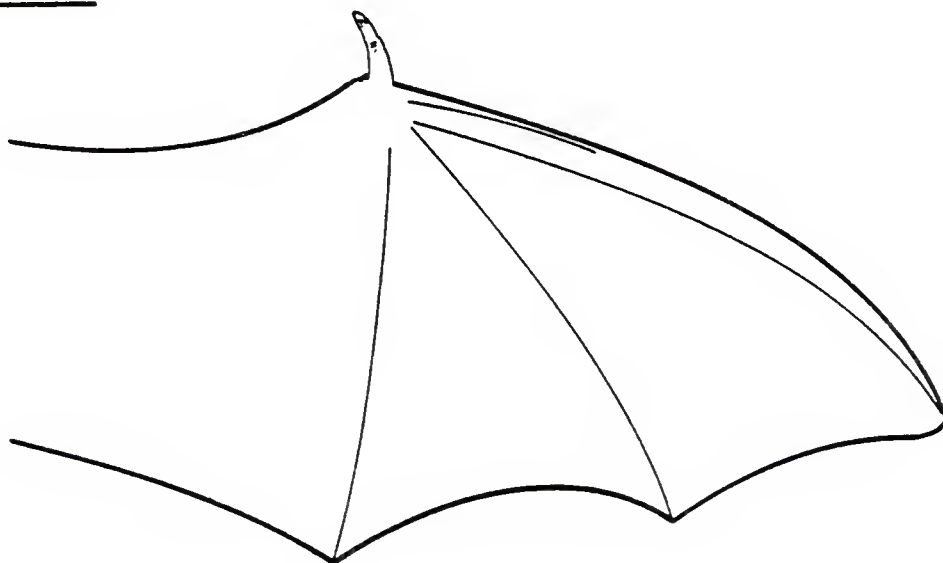
The flight speeds observed in the present study are similar to those observed in Plecotus auritus by Norberg (1976). In her study, the bats were filmed while flying unrestrained within a room and flight speeds ranged between 2 a 3 m/sec. Higher velocities were exhibited by Noctilio albiventris (3.51-10.38 m/sec) and Tadarida brasiliensis (4.33-9.40 m/sec) while flying in a wind tunnel (Brandon, 1979). Leptonycteris sanborni, a facultative hovering bat, flew between 2.0 and 6.0 m/sec in a wind tunnel study. The higher speeds reported in the wind tunnel studies were not duplicated in the present study. Predictable flight, suitable for EMG analysis, was facilitated by filming the bats shortly after takeoff and before they reached maximum velocities. Also, it is not known if Artibeus is capable of flying up to 4.47 m/sec as was generalized for many bats (Hayward and Davis, 1964).

The path of the wingtip during the wingbeat cycle changes with increasing airspeed. During slow flight in Plecotus auritus, the wingtip path was directed upwards and caudally relative to still air during the upstroke (Norberg, 1976). At higher velocities (2-2.5 m/sec), the upstroke of Plecotus was directed almost vertically, and at higher velocities (greater than 3.0 m/sec) exhibited a cranial and dorsal movement relative to still air. The same tendency was present in Artibeus flying between 2-2.85 m/sec. The wing was directed

caudally during the upstroke at low speeds (Figure 2) and more vertically during the upstroke at higher velocities (Figure 3). If wing movements are different at several airspeeds, these relationships must be considered when evaluating EMG recordings. The difference in wing movements may be correlated with differences in muscular activity.

Flying animals have been classified according to several descriptors of wingshape including the aspect ratio (Saville, 1962). Vaughan (1959) discussed the relationship between aspect ratio and foraging habits. Struhsaker (1961) was the first author to describe the aspect ratios of a diversity of chiropteran wings. Aspect ratios were also provided for bats by Farney and Fleharty (1969), Findley et al. (1972), Lawlor (1973), Smith and Starrett (1979), and Norberg (1981). My calculation of an aspect ratio for Artibeus jamaicensis, 6.67, is slightly greater than but comparable to the value of 6.36 obtained by Norberg (1981). In general, bats with low aspect ratios are common in heavily forested habitat, whereas high aspect ratio bats are commonly associated with flight in open, uncluttered airspace (Findley et al., 1972). For example, Vaughan (1959) compared the high-altitude flight of Eumops perotis with that of swifts. These bats fed high over the forest canopy at high airspeeds. Vaughan reported that the aspect ratio of Eumops was 11.9, the highest value among the three species that he studied. Intermediate aspect ratio wings are not well correlated with any particular behavioral repertoire or foraging environment (Norberg, 1981). Wing shape in Artibeus probably evolved

Figure 5.--High- and low-aspect ratio wingshapes. Tadarida brasiliensis (Molossidae) exemplifies the long and narrow outline of a high aspect ratio wing. In contrast, the wing of Artibeus jamaicensis exhibits a lower aspect ratio, characterized by a broad and stubby appearance.

TadaridaArtibeus

in response to the needs of the bat in carrying large food items and transporting infants. Artibeus females have been observed carrying young weighing 10.0 g (personal observation). Low aspect ratio wings promote increased lift at lower flight speeds (Findley et al., 1972), permitting more careful scrutiny of potential food or of potential feeding sites. Maneuverability does not appear to be characteristic of the flight pattern of Artibeus in comparison with some more agile bats. This was supported by repeated netting success while trying to collect bats in mist nets (personal observation). In contrast, other phyllostomids such as Micronycteris have low aspect ratio wings (Smith and Starrett, 1979) and were frequently observed eluding my nets during field work in Venezuela.

Wing loading is an estimate of the relationship between the weight of a bat and the lift-producing potential of a wing. To fly slowly, which would be adaptive to an Artibeus investigating a fig tree as a potential food source, two strategies might be employed: the species might exhibit low body weight or a greater airfoil surface area (Findley et al., 1972). My data for wing loading in Artibeus were slightly less than the 16.65 N/m^2 reported by Norberg and greater than the 15.94 N/m^2 reported by Smith and Starrett (1979). Norberg found that the wingloading of frugivorous microbats (this included most phyllostomid fruit eaters) was intermediate between the insectivorous Molossidae and Vespertilionidae. The molossids of equivalent weight have high aspect ratios and must maintain high airspeeds to avoid a

stall (Vaughan, 1966; Norberg, 1981). In contrast, the vespertilionids generally have a large wing area for a given body size (Norberg, 1981) and fly at relatively lower airspeeds than similar-sized molossids (Hayward and Davis, 1964; Brandon, 1979). Thus, the wing of Artibeus represents a compromise between the two strategies suggested by Findley et al. (1972). The bats have large body weights but have not substantially increased wing surface area like vespertilionids have. This combination leads to reduced maneuverability, different from the butterfly-like flight observed in some vespertilionids. Also, I have never observed Artibeus hovering. The bats tend to fly directly along aerial pathways to and from a feeding tree, and fly past a tree several times when investigating or searching for food.

In conclusion, the wing of Artibeus represents a generalized condition relative to certain other bats. I suggest that this reflects the heterogeneous nature of the airspace through which the bat must travel every night. A high aspect ratio wing is not suited to travel through the cluttered environment of most neotropical forests. Also, at slow airspeeds, the larger lift production that accrues from a low aspect ratio wing permits the bat to forage upon and to transport large energy-rich foods. A secondary consequence of the large body mass and low aspect ratio of Artibeus may relate to post-natal development and maternal care of the young bats.

OSTEOLOGY

Results

Clavicle

The clavicle in five specimens had a mean length of 16.10 mm and a mean diameter at the midshaft of 1.15 mm. The bone articulates proximally with the manubrium by a synovial joint. Distally, the clavicle articulates with the scapula both by a synovial joint at the base of the coracoid process and by a ligamentous connection with the tip of the acromian process. Viewed cranially, the bone is straight, with slight lateral curvature near its distal end. Viewed laterally, the bone has a slight caudal curvature at the distal end. The distal one-third of the cranial border of the bone is expanded for insertion of part of the subclavius muscle. In lateral view the distal end of the bone lies cranial relative to the proximal end.

Scapula

The scapula is a thin, relatively flat bone positioned over the dorsal surface of the cranial part of the ribcage. It articulates proximally with the clavicle as described above. The scapula

Figure 6.--Lateral view of the thoracic and axillary skeleton. UF 16265.

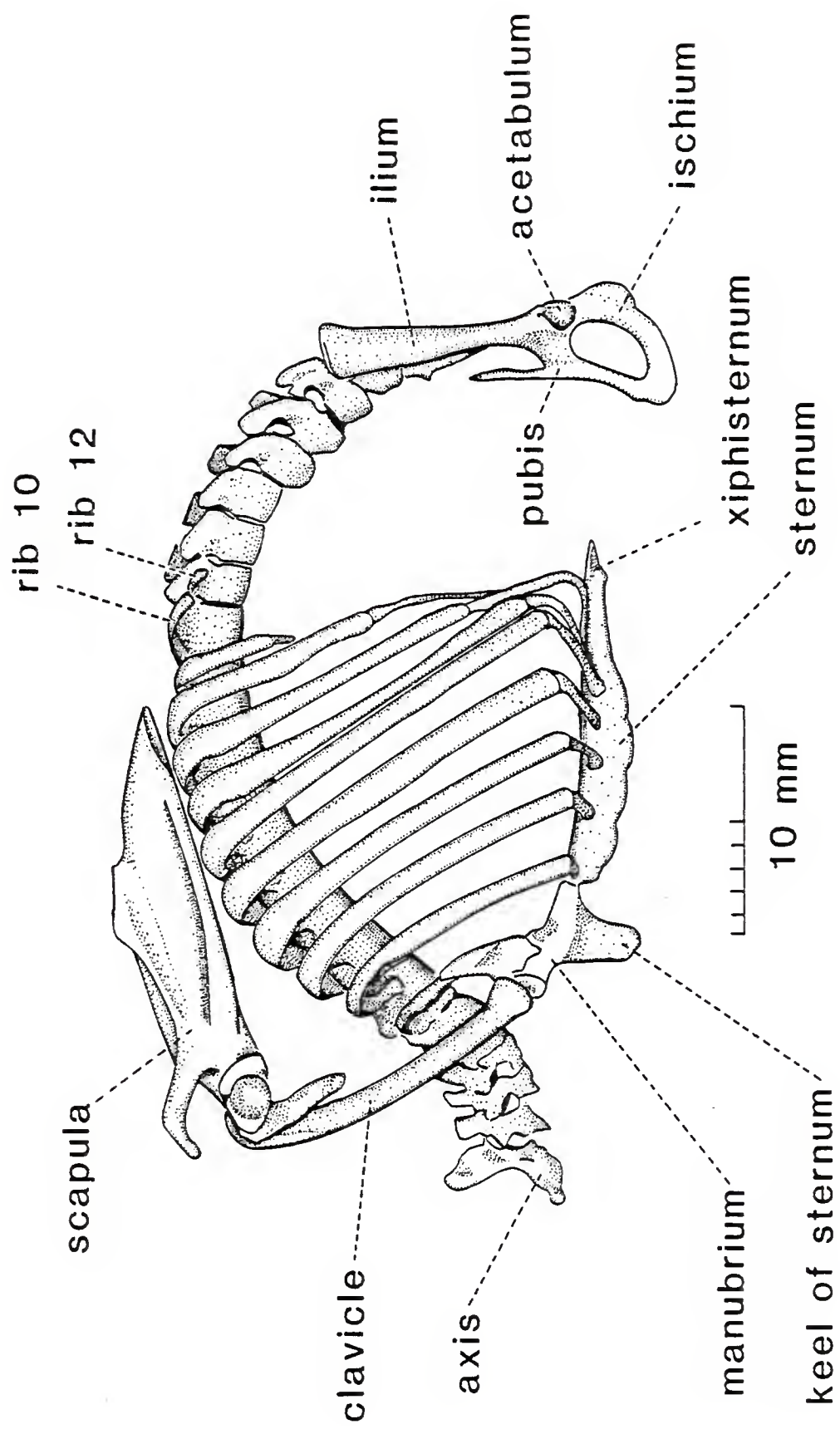
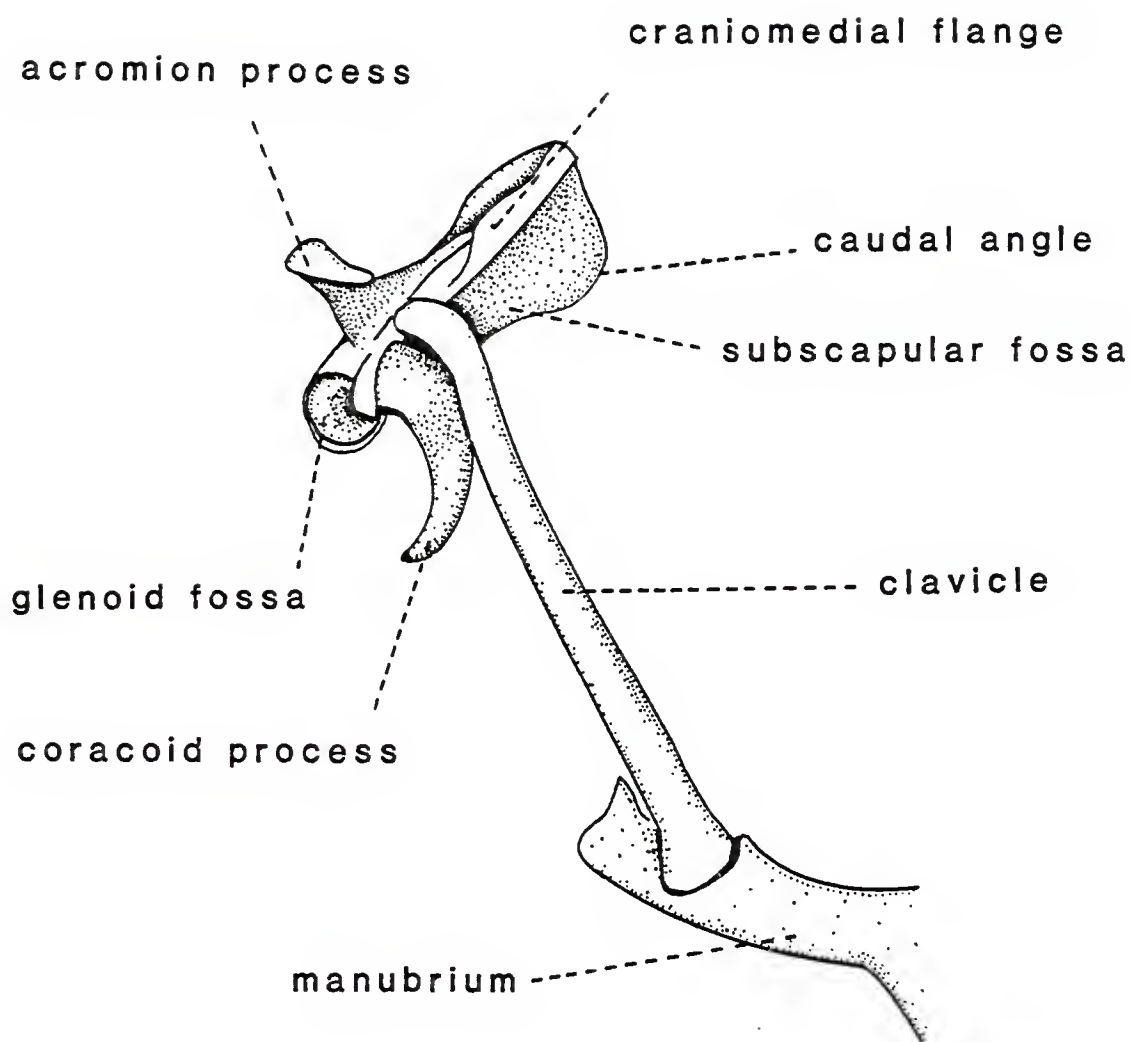
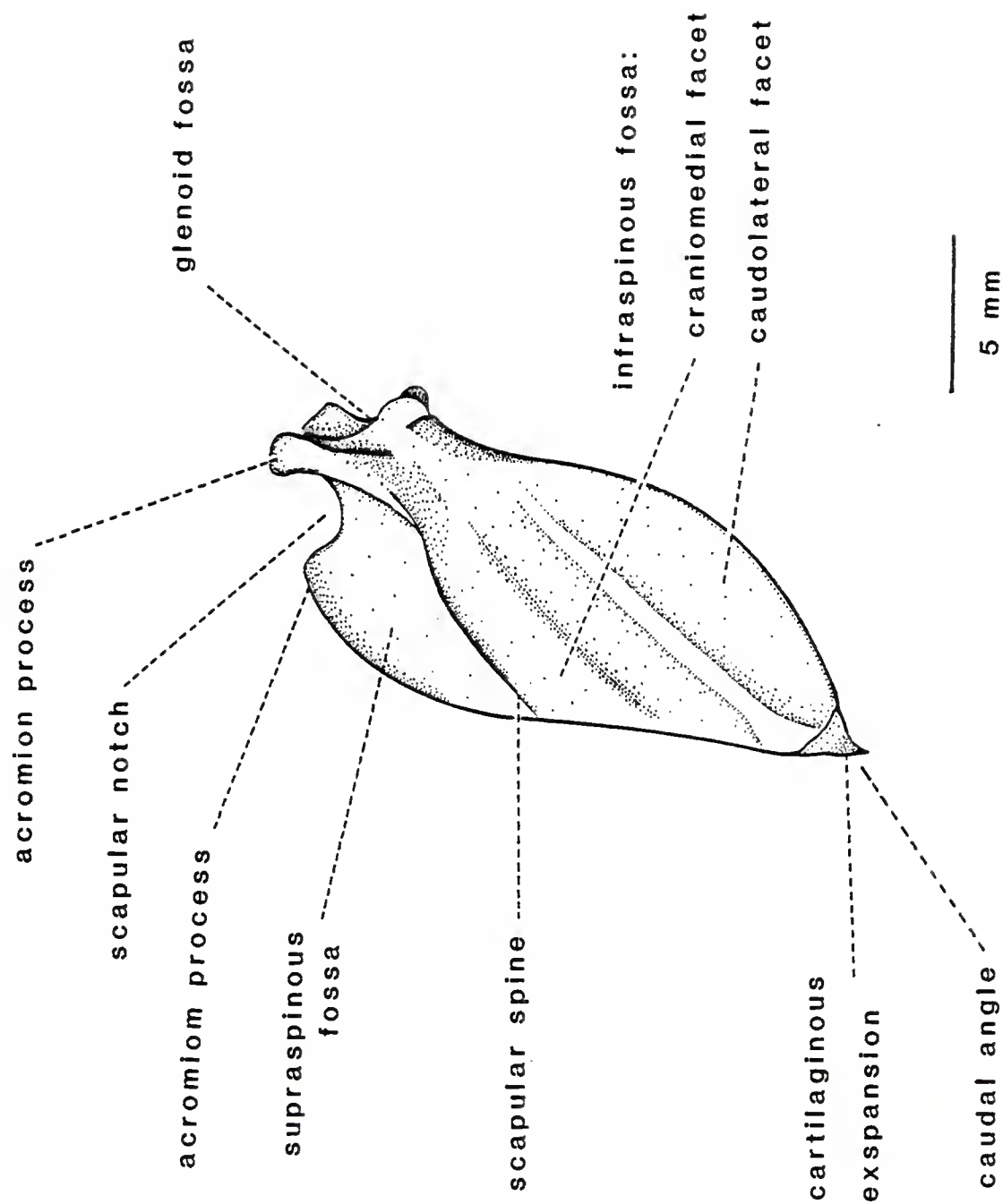


Figure 7.--Cranial view of the right pectoral girdle.
UF 16265.



5 MM

Figure 8.--Dorsal view of the scapula. UF 16265.



articulates with the humerus at the glenoid fossa, which forms the shoulder joint. The dorsal surface of the scapula is divided into two major subdivisions by the scapular spine. Cranially, the supraspinous fossa forms a small flat shelf immediately cranial to the scapular spine. Caudal to the scapular spine is the infraspinous fossa which is, in cranial to caudal sequence, divided into three subdivisions: craniomedial facet, intermediate facet, and caudolateral facet. The ventral surface of the scapula is the subscapular fossa, composed of two concave facets. The cranial subscapular facet corresponds with the contours of the combined supraspinous fossa and craniomedial facet of the dorsum. The caudal facet of the subscapular fossa corresponds with the contours of the combined intermediate and caudolateral facets of the dorsum. There are two borders on the scapula. Medially, the vertebral border lies in a sagittal plane extending from the caudal angle to the scapular spine. Cranial to the scapular spine, the vertebral border curves laterally and becomes continuous with the craniomedial flange of the scapula. On the lateral aspect of the scapula, the axillary border is convex, coursing cranially from the caudal angle to the glenoid fossa. The infraglenoid tubercle is a small projection from the axillary border 1-5 mm caudal to the glenoid fossa. The supraglenoid fossa is slightly concave and lies between the glenoid fossa and the dorsal base of the coracoid process. This surface abuts with the greater tubercle of the humerus when the wing is fully abducted.

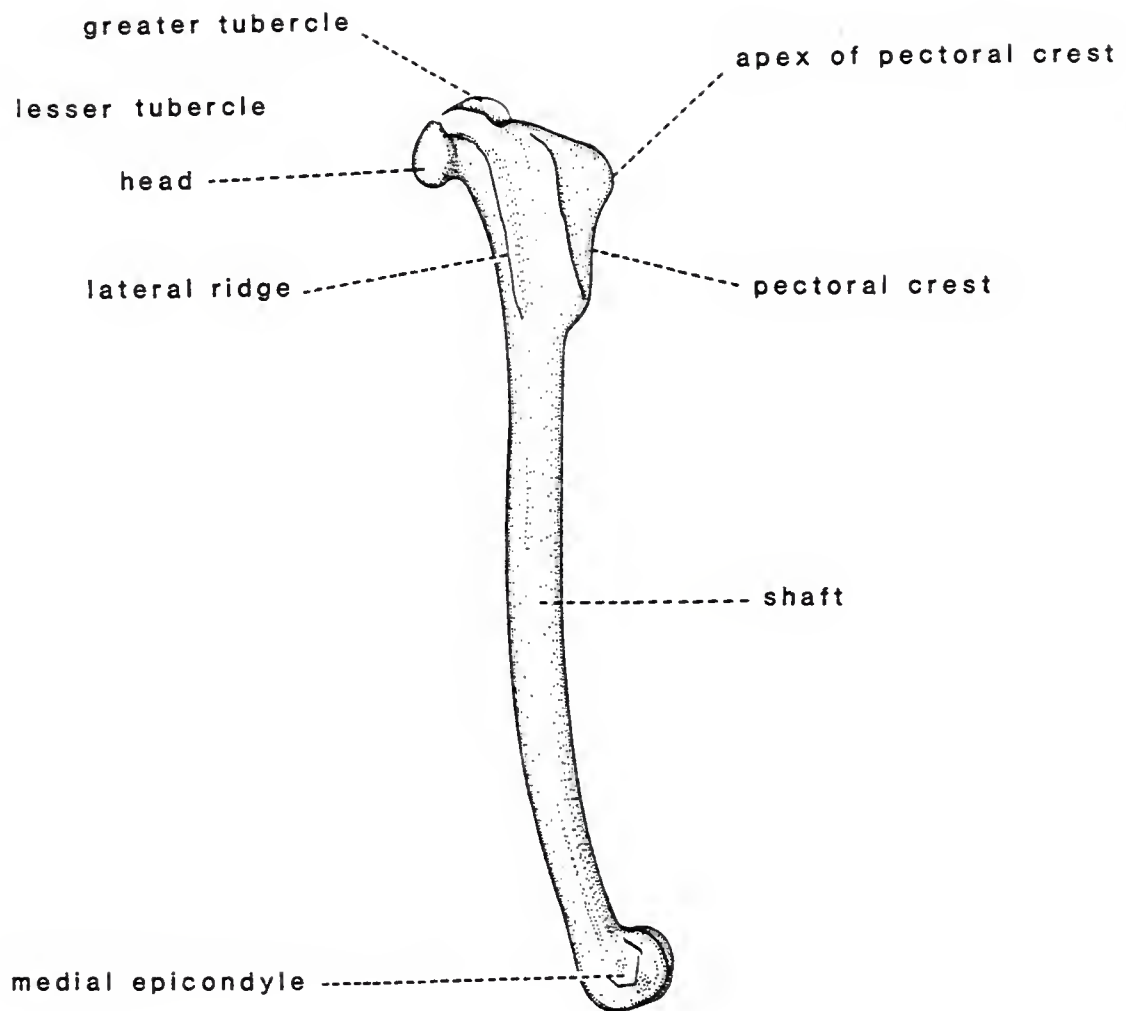
Several processes are evident on the scapula of Artibeus. The cartilaginous expansion is triangular and projects from the caudal angle and curves ventrally. The acromion process projects cranially and dorsally from the scapular spine, and curves cranially. A 2 mm long flared part of the acromion process lies dorsal to the clavoscapular articulation. The coracoid process extends cranially and ventrally from the supraglenoid region of the scapula and curves laterally to terminate 2 mm ventral to the glenoid fossa.

Humerus

The humerus averaged 31.90 mm in length (measured between the articular surfaces) and 1.98 mm in diameter (along the craniocaudal axis) at the midshaft. In cranial view the distal end of the shaft curves slightly lateral. The shaft is unmarked. Both ends of the humerus are modified to form articular surfaces and to accommodate muscle attachments.

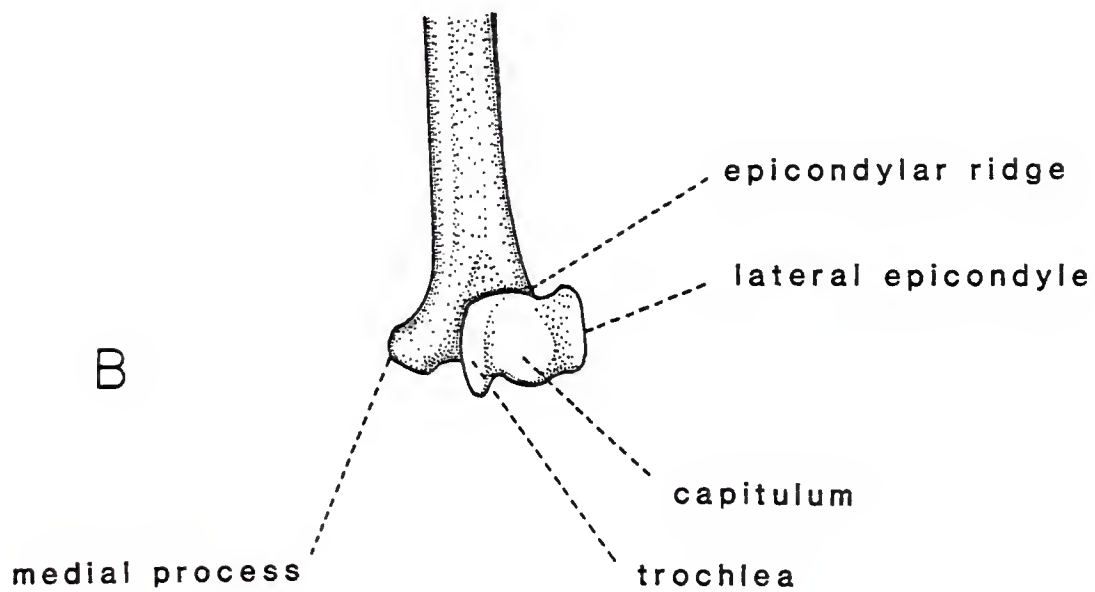
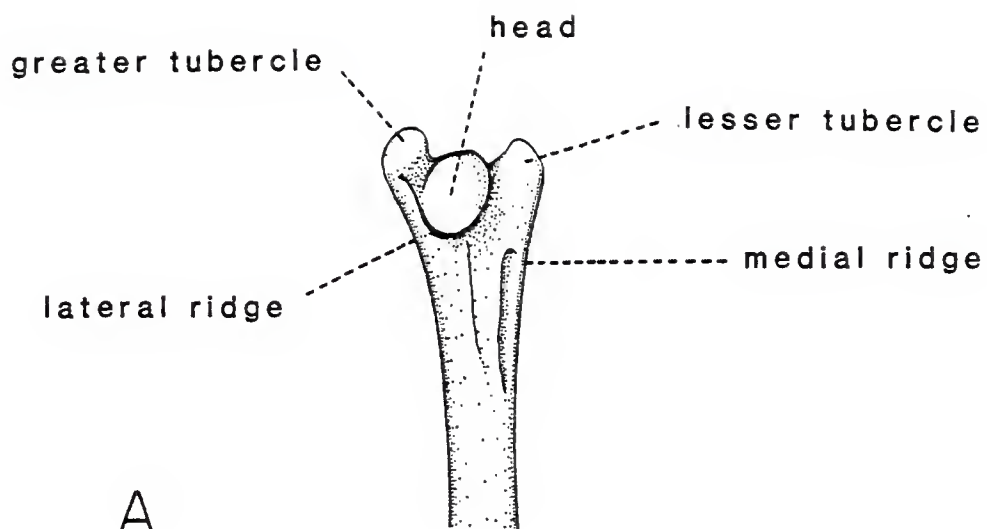
The shoulder joint is formed in part by the head of the humerus. The head is a convex elliptical surface that articulates proximally with the glenoid fossa. The greater tubercle lies lateral to the head and projects 1 mm proximally. The greater tubercle provides attachment for the suprascapular muscles and abuts with the supraglenoid fossa of the scapula when the humerus is fully abducted. This lock occurs when the humerus is abducted about 32 degrees dorsal to the horizontal plane of the scapula. The lesser tuberosity also extends slightly proximal to and lies on the medial aspect of the head. Several ridges extend

Figure 9.--Medial view of the left humerus. UF 16265.



5 MM

Figure 10.--Articular surfaces of the humerus. (A) Caudal aspect of the proximal left humerus. (B) Cranial aspect of the distal left humerus. UF 16265.



distally from the lesser and greater tuberosities. From the lesser tuberosity, the medial ridge extends 6 mm along the proximal medial border of the humerus and serves as the point of attachment of the teres major and latissimus dorsi muscles. A second indistinct ridge crosses the proximal surface of the humerus and courses along the base of the ventral surface of the pectoral ridge. This ridge is the site of insertion of the pectoralis abdominalis. The lateral ridge is a small indistinct ridge on the lateral surface of the humerus courses 7 mm distal to the greater tuberosity. This forms the dorsolateral border of the origin of triceps brachii, lateral head. The most prominent ridge from the greater tuberosity is continuous distally with the pectoral ridge, a large flat projection on the lateral aspect of the humerus. The pectoral ridge extends 8 mm along the lateral edge of the humerus. The widest portion of the pectoral ridge, 2-4 mm distal to the head, is termed the apex. The pectoral ridge provides insertion sites for the pectoralis muscles medially, and the deltoid muscles laterally.

At the elbow the radius articulates with the cranial surface of the humerus. The ulna articulates along the distal and caudal surface of the humerus. The capitulum and trochlea are fused cranially to present a synovial surface for the humeroradial articulation. The trochlea extends around the distal and caudal surface of the humerus to provide an articular surface for the ulna. Medial to the trochlea and composing one-third of the distal end of the bones is a medial

process. This region provides an attachment surface for several flexor muscles of the antebrachium. On the lateral end of the capitulum is the spool-shaped lateral epicondyle. Extending from the lateral epicondyle proximally onto the shaft of the humerus is the short epicondyle ridge. The lateral epicondyle and epicondylar ridge provide an area of attachment for several antebrachial extensor muscles. The elbow articulation is not a pure hinge joint. Slight rotation of the radius relative to the capitulum is evident in fresh specimens of Artibeus.

Radius

The radius is slightly curved along its length. In five specimens, the mean length is 53 mm. At the midshaft, it is thickest in the dorsoventral axis (1.8 mm) to resist bending forces associated with the wingbeat cycle. The proximal articular region is thickened to provide a surface for articulation with the humerus and to provide a strong site for attachment of the biceps brachii. The distal articular region is wide and flat. This provides a structural mechanism for separation of the tendons of insertion of the antebrachial muscles and increases the mechanical advantage of several of these muscles as they cross the carpus.

The proximal articular surfaces is oriented cranially and includes a large concave fossa for articulation with the capitulum. Laterally a smaller elliptical concavity articulates with the trochlea. A ridge on the caudal aspect of the radius courses 5 mm distal from the elbow

joint. A ridge on the medial aspect of the proximal radius courses 3 mm distal to the elbow joint and provides the site for insertion of the biceps brachii.

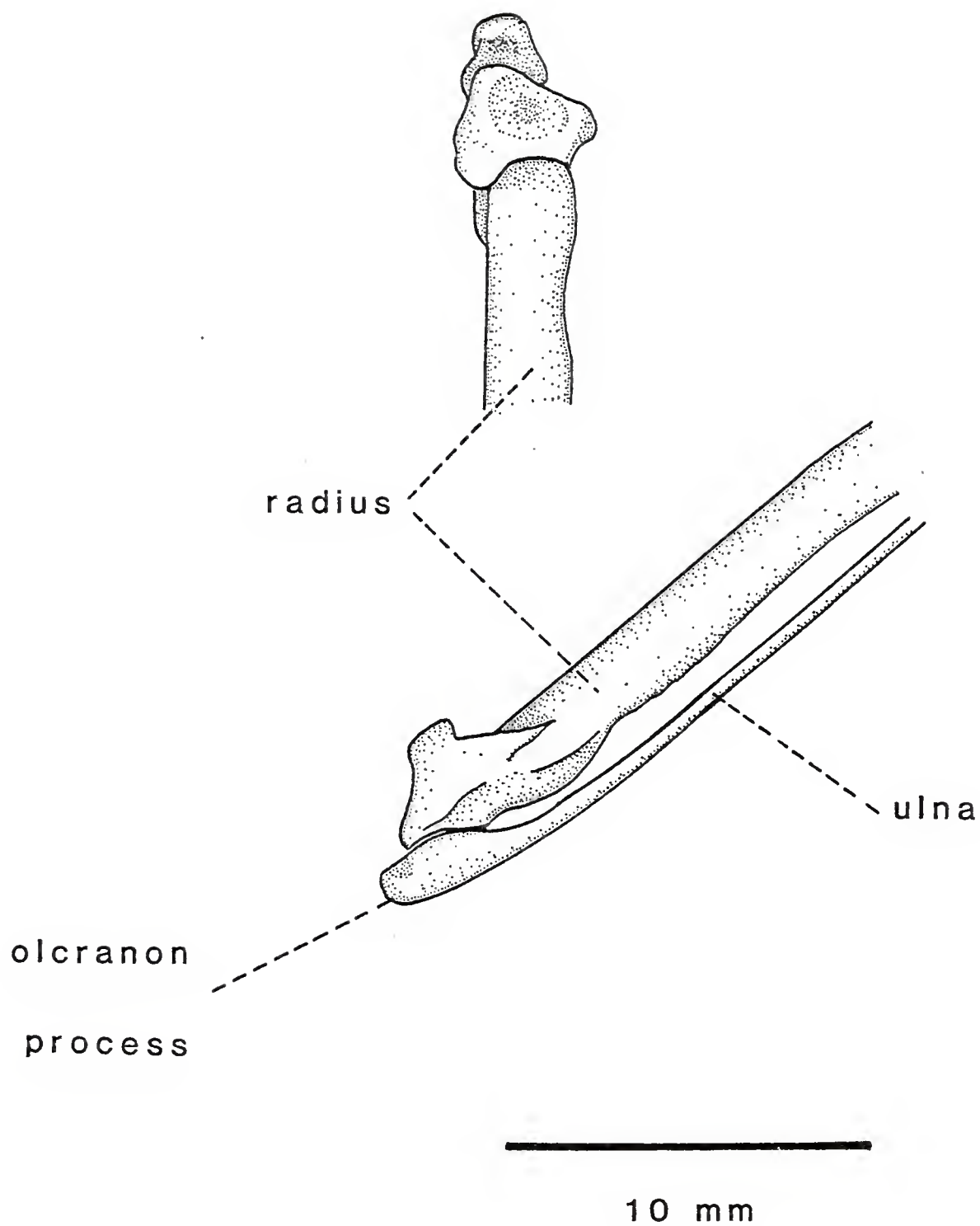
The styloid process and pseudostyloid process are small bumps on the distal articular end of the radius but are not greatly developed in bats. The pseudostyloid process is on the medial side of the distal articular surface, analogous in position to the styloid process of the ulna in other mammals.

The axis of the distal articular surface is laterally rotated about 20 degrees from the orientation of the proximal articular surface. The distal articular surface presents a concave surface for articulation with the proximal carpal bones. When the wing is laterally outstretched, the radiocarpal joint permits flexion and extension in a mediolateral plane and no movement in the dorsoventral plane. This restriction braces the joint against displacement caused by the force of the airstream.

Ulna

The ulna is reduced in bats to a length approximately one-half the length of the adjacent radius. The proximal articular surface comprises the cranial surface of the olecranon process and articulates with the caudal extension of the trochlea of the humerus. An interosseous membrane is found between the radius and ulna. The ulna tapers towards its distal articulation with the radius and presents no processes.

Figure 11.--Dorsal view of the radius and ulna.



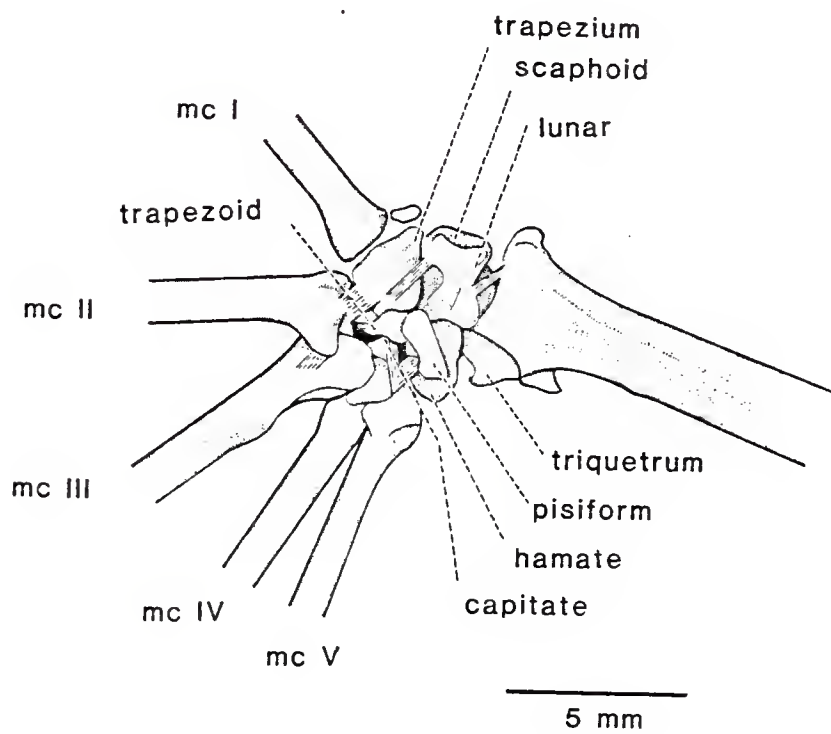
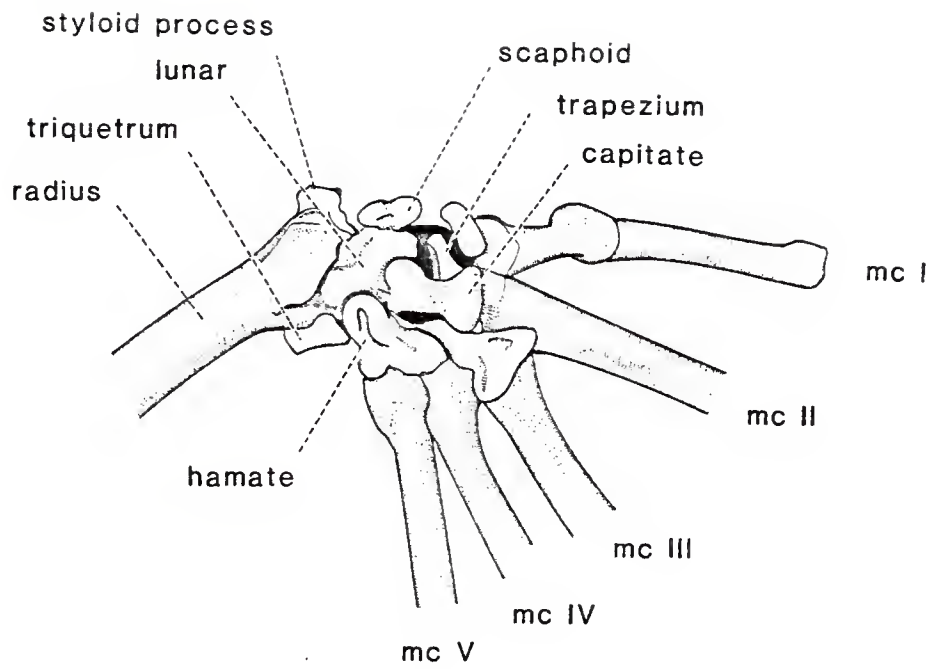
Manus

The diminutive size of and the tightly bound joint cavities between the bones of the carpus make it difficult to adequately describe the bones of this region. A perspective on the carpal anatomy can be obtained by studying Figure 12. The carpus of Artibeus includes eight bones as is typical of many mammals.

The proximal row of carpal bones includes the scaphoid, lunar, and triquetrum. The largest carpal bone, the lunar, articulates proximally with the radius and distally with the trapezoid, trapezium, and capitate. On the lateral aspect of the distal articular surface of the radius, the triquetrum (=cuneiform of Vaughan, 1959) is bound to the radius and forms the caudoventral border of the canal traversed by the antebrachial extensor muscles. The scaphoid is a small bone located craniodorsally in the carpus along the cranial surface of the lunar. The scaphoid, unlike the lunar and triquetrum, is not bound to the distal surface of the radius.

The distal row of carpal elements includes the trapezium, trapezoid, capitate, hamate, and pisiform. The trapezium articulates with the proximal bases of metacarpals I and II, and with the craniodistal surface of the lunar. The trapezoid is compressed craniocaudally and articulates with the proximal base of metacarpal II. The capitate (=magnum of Vaughan, 1959) is a large bone that has an hourglass shape when viewed dorsally. It articulates with the proximal bases of metacarpals II and III. Lateral to the capitate, the

Figure 12.--Dorsal and ventral views of the carpus.



hamate (=unciform of Vaughan, 1959) articulates distally with the bases of metacarpals IV and V, and proximally with the lunar and triquetrum. The pisiform is a small rod-shaped bone on the palmar surface of the carpus and is firmly bound to the ventral surface of the capitate and hamate.

The distal part of the wing is supported by digits II through V. The metacarpals diverge within the wing membrane and are the largest elements in each digit. Movement at the carpometacarpal joints of digits II through V is restricted to flexion and extension. Flexion of the carpometacarpal joints brings the digits parallel to and into juxtaposition with the radius. The metacarpophalangeal and interphalangeal joints permit only palmar flexion or dorsiflexion. These movements adjust the camber of the wing during the wingbeat cycle. Digit II has one phalanx. Digits III through V have three phalanges. Digit I, the pollex, is unique because of the range of motion possible at the carpometacarpal joint. Besides flexion and extension, the pollical carpometacarpal joint permits the extensive rotation necessary for use of the pollex in several functions: the pollex is a prehensile organ used during landing maneuvers or while manipulating food. The second phalanx of the pollex bears a claw. The proximal and second phalanges of the pollex are both free of the leading edge of the dactylopatagium minus and the propatagium.

MYOLOGY

Trapezius Group

Clavotrapezius and Acromiotrapezius

Form. The clavotrapezius originates by a fibrous attachment on the dorsal surface of the seventh cervical vertebrae. Fibers of acromiotrapezius arise from the dorsal surfaces of thoracic vertebrae one through six. There is no apparent separation between adjacent fibers of the clavotrapezius and acromiotrapezius. Insertion of the clavotrapezius is by fibers on the distal 2.5 mm of the craniomedial surface of the clavicle. The acromiotrapezius inserts separately from the clavotrapezius: insertion is by fibers convergent upon the anterior and dorsal surface of the acromion process and on a muscular raphe caudal to the acromion process. Innervation of both muscles is by cranial nerve XI (spinal accessory nerve).

Comparative aspects. The clavotrapezius and acromiotrapezius muscles have been treated as two separate muscles in the Phyllostomidae (Macalister, 1872; Walton, 1967), and also in the specialized vampire bats (Altenbach, 1979). In contrast, the condition observed in many other bats, including phyllostomatids, demonstrated fusion of these two bellies (Strickler, 1978; Vaughan, 1959, 1970_a). In the three species he studied, Vaughan (1959) noted the fusion of the two bellies only in

Macrotus (Phyllostomidae). Macalister (1872; p. 138) most likely made reference to the clavotrapezius of Artibeus sp. when he described "a semi-detached upper slip passed from the two lowermost cervical spines to the outer fifth of the clavicle." The two muscles are distinguishable in Artibeus only by a fascial division coursing from the C7-T1 articulation to the distal end of the clavicle. Despite their separate insertion, I consider the two muscles to be fused and to share a similar function. The clavotrapezius and acromiotrapezius form a flat sheet of parallel fibers, thickest at the cranial end (clavotrapezius portion).

Functional aspects. The clavotrapezius and acromiotrapezius exhibit a similar pattern of EMG activity during the wingbeat cycle. Clavotrapezius has a major period of EMG activity during the transition between the late downstroke and early upstroke. A second period of activity occurs during the middle to late upstroke phase, but the myopotentials have less than one-half of the amplitude observed during the earlier EMG burst. Acromiotrapezius also has two periods of EMG activity, but both exhibit similar amplitude and frequency. The first period of activity in acromiotrapezius precedes clavotrapezius activity by approximately 10 m/sec. Both muscles are anatomically positioned to effect the upstroke by drawing the scapula medially (Vaughan, 1959; Strickler, 1978; Altenbach, 1979). The primary activity of each muscle contributes to this upstroke function. The secondary burst of activity possibly stabilizes the scapula in response to the adductor activity of

Figure 13.--Dorsal view of the shoulder and arm of Artibeus jamaicensis.
Superficial muscles are exposed on the left, and deeper muscles of the
back and shoulder are exposed on the right.

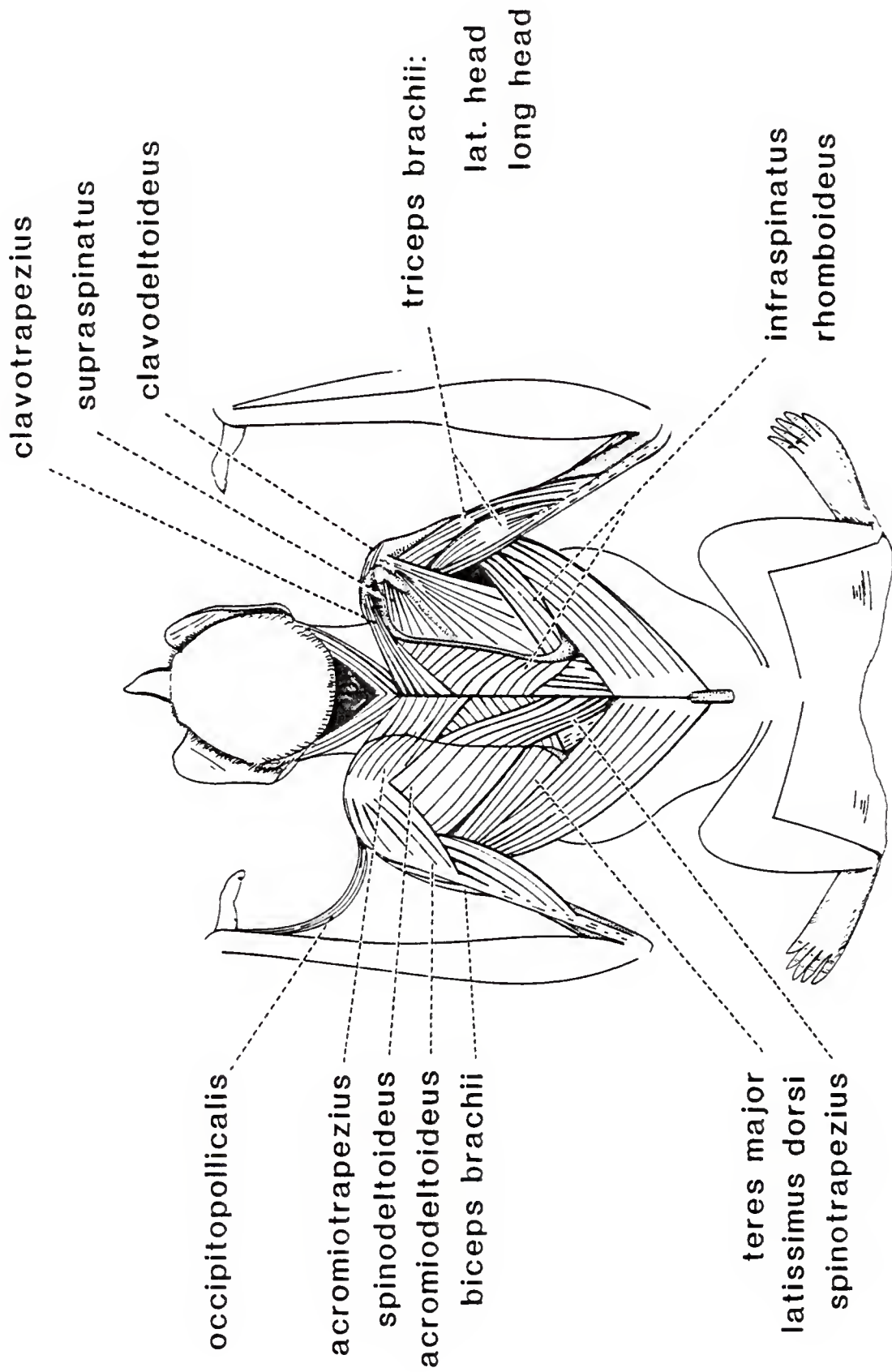


Figure 14.--Activity patterns of shoulder and arm muscles in Artibeus jamaicensis during slow flight. Black bars indicate observed periods of high-amplitude activity. Unshaded bars indicate observed periods of muscle activity that were consistently one-half of the amplitude exhibited in high-amplitude sequences. Vertical lines are placed one standard deviation from the means of activity onset and termination. Small arrows indicate mean downstroke duration for each muscle experiment.

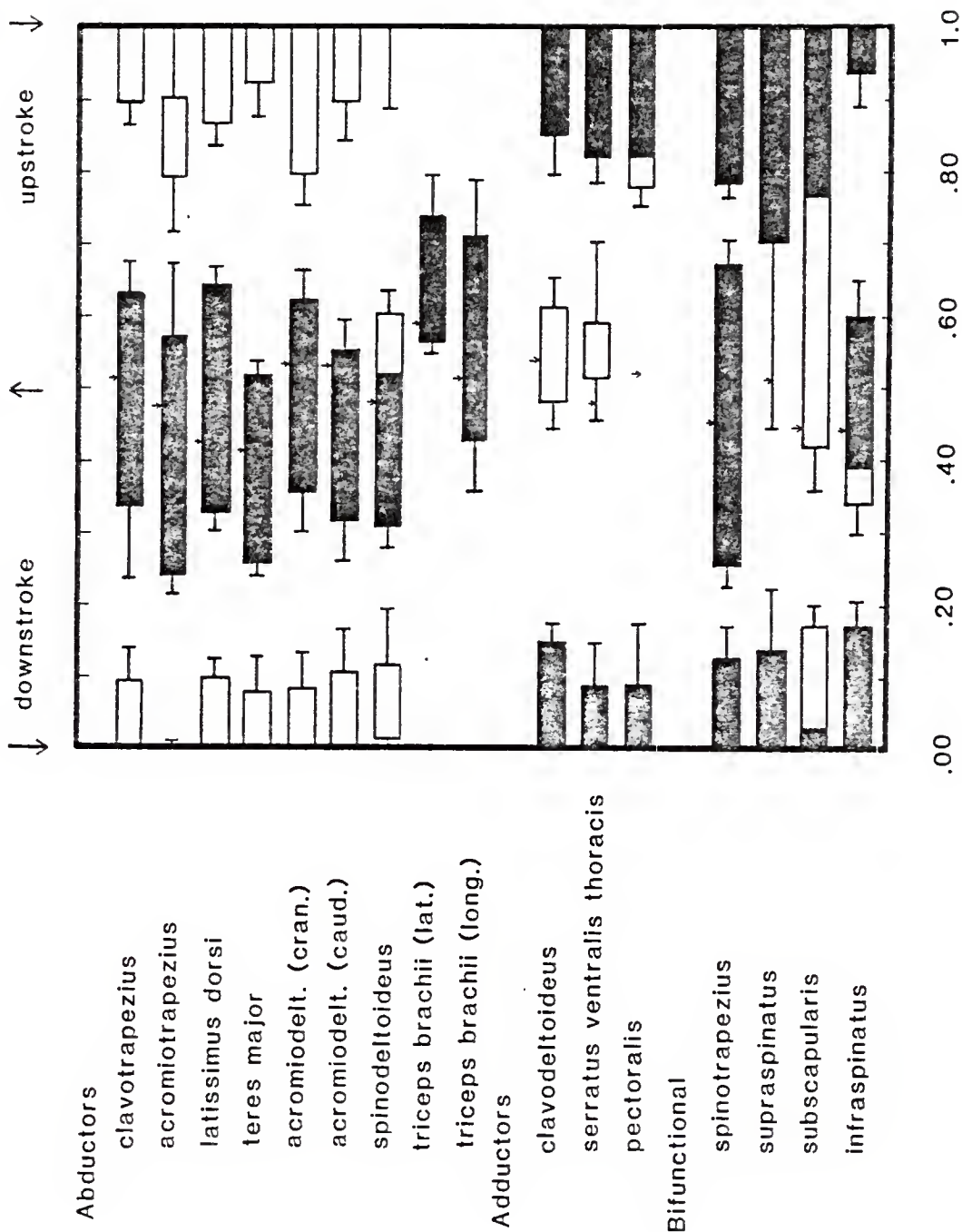


Table 2.--Electromyographic data for activity patterns of the shoulder musculature in Artibeus jamaicensis during slow flight. N= number of wingbeats analyzed per muscle. Mean duration of the downstroke is expressed as a percentage of the wingbeat cycle duration. Mean times of muscle activity onset and termination are recorded in relation to the wingbeat cycle from 0.00 to 1.00, and one standard deviation is recorded.

Muscle	N	Downstroke Duration	Onset Time (S.D.)	Termination Time (S.D.)
ABDUCTORS				
Clavotrapezius	12	0.515	0.332 (.099) 0.894 (.030)	0.631 (.045) 0.092 (.047)
Acromiotrapezius	9	0.477	0.236 (.033) 0.794 (.080)	0.572 (.104) 0.903 (.104)
Latissimus dorsi	13	0.428	0.329 (.028) 0.869 (.035)	0.644 (.025) 0.098 (.025)
Teres major	3	0.412	0.259 (.022) 0.922 (.046)	0.519 (.016) 0.077 (.045)
Acromiodeltoideus cranial	10	0.536	0.355 (.056) 0.799 (.041)	0.628 (.040) 0.081 (.055)
caudal	10	0.532	0.315 (.053) 0.894 (.051)	0.556 (.062) 0.103 (.065)
Spinodeltoideus	11	0.481	0.309 (.030) 0.001 (.115)	0.608 (.030) 0.114 (.080)
Triceps brachii lateral	3	0.594	0.564 (.017)	0.741 (.053)
long	15	0.513	0.429 (.069)	0.714 (.074)

Table 2.--continued

Muscle	N	Downstroke Duration	Onset Time (S.D.)	Termination Time (S.D.)
<u>ADDUCTORS</u>				
Clavodeltoideus	19	0.544	0.853 (.059) 0.481 (.038)	0.135 (.027) 0.617 (.039)
Serratus ventralis	11	0.484	0.823 (.036) 0.515 (.058)	0.091 (.058) 0.599 (.109)
Pectoralis	7	0.526	0.781 (.027)	0.094 (.086)
<u>BIFUNCTIONAL</u>				
Spinotrapezius	7	0.452	0.254 (.031) 0.784 (.020)	0.672 (.032) 0.123 (.047)
Supraspinatus	6	0.518	0.706 (.263)	0.142 (.084)
Infraspinatus	7	0.449	0.346 (.039) 0.942 (.059)	0.607 (.046) 0.120 (.039)
Subscapularis	10	0.450	0.420 (.060)	0.174 (.033)

the early downstroke, or causes active lengthening of the pectoralis fibers during their early period of activity. Similar passive lengthening, or "eccentric contractions," increased force production of several locomotory muscles in other animals (Cavagna et al., 1977; Heglund et al., 1979; Goslow et al., 1981). The biphasic activity observed in Artibeus contrasts with the single EMG burst observed in Antrozous (Hermanson and Altenbach, 1983). The heavier wingloading of Artibeus may necessitate the extra muscular activity. In conclusion, both clavotrapezius and acromiotrapezius show abductor activity, but at slightly different times in the wingbeat cycle. The secondary activity in each muscle stabilizes the scapula against the force of the adductors.

Spinotrapezius

Form. The spinotrapezius originated by fibers on the dorsal midline over lumbar vertebrae two through three. It inserts by an aponeurosis on the vertebral border of the scapula, extending from the caudal angle to the point 2 mm anterior to the scapular spine. The spinotrapezius is a thin, parallel-fibered muscle. Based upon its anatomy, the muscle tips the vertebral border of the scapula ventrally, and retracts the scapula (Strickler, 1978). Innervation is by the spinal accessory nerve.

Functional aspects. Spinotrapezius exhibits biphasic EMG activity. Both periods of activity have approximately equal amplitude and frequency characteristics. One period commences at 0.254 and

terminates at 0.672: This contributes to the overall abduction of the wing along with the activity of clavotrapezius and acromiotrapezius. A second period of activity commences at 0.784 and terminates at 0.123 of the following wingbeat. Spinotrapezius is quiescent only during about 24 percent of the wingbeat, an observation similar to EMG data from Desmodus (Altenbach, 1979), but in contrast to the shorter, single activity period observed in Antrozous (Hermanson and Altenbach, 1983). The extent of EMG activity throughout the wingbeat suggests a multiple function for spinotrapezius as proposed by Vaughan (1959): stabilization of the scapula and abduction of the wing and scapula are likely functions.

Costo-spino-scapular Group

Serratus Ventralis Cervicis

The serratus ventralis cervicis was previously called the levator scapulae in the chiropteran anatomy literature.

Form. The serratus ventralis cervicis originates from fibrous attachments along the dorsolateral aspect of the transverse processes of cervical vertebrae three through six. The muscle has a fleshy insertion on the ventral surface of the craniomedial flange of the scapula, and along the vertebral border of the scapula cranial of the scapular spine. The muscle is composed of two parallel-fibered slips: the cranial slip originated from cervical vertebrae three and four, and the caudal slip from five and six. Innervation is by a branch of the dorsal scapular nerve, and by cervical nerve five.

Comparative aspects. In many mammals, the serratus ventralis is composed of a continuous sheet of muscle, including fibers that originate from the cervical vertebrae (serratus ventralis cervicis) and from the lateral surface of the ribcage (serratus ventralis thoracis). The terminology and comparative anatomy are discussed with the serratus ventralis thoracis.

Strickler (1978) noted that although the cranial origin normally extends to cervical vertebra five to seven the origin of serratus ventralis cervicis varies in bats. Phyllostomoids were characterized by a relatively large insertion, usually extending along the vertebral border of the scapula caudal to the scapular spine. Walton (1967) observed a similar insertion in Artibeus lituratus extending along the "coracoid border" and vertebral border of the scapula to a point immediately posterior to the spine.

Walton (1967) described the serratus ventralis cervicis of A. literatus to be composed of three large slips. Macalister observed only two slips in Artibeus sp. (Macalister, 1872). I concur with Macalister.

Functional aspects. Strickler (1978) concluded that a correlation existed between degree of humeroscapular "locking" observed in some bats and the size of the serratus ventralis cervicis muscle. He observed that this muscle was relatively enlarged while the rhomboideus was relatively small in vespertilionids and phyllostomatids. In contrast, the serratus ventralis cervicis was small and the

rhomboideus large in emballonurids and pteropodids. These two groups possess poorly developed humeroscapular locking mechanisms (Vaughan, 1970a, 1970b; Strickler, 1978). Strickler suggested that the major role of serratus ventralis cervicis is to stabilize the medial border of the scapula against rotation about its longitudinal axis. No EMG data are available to test this hypothesis.

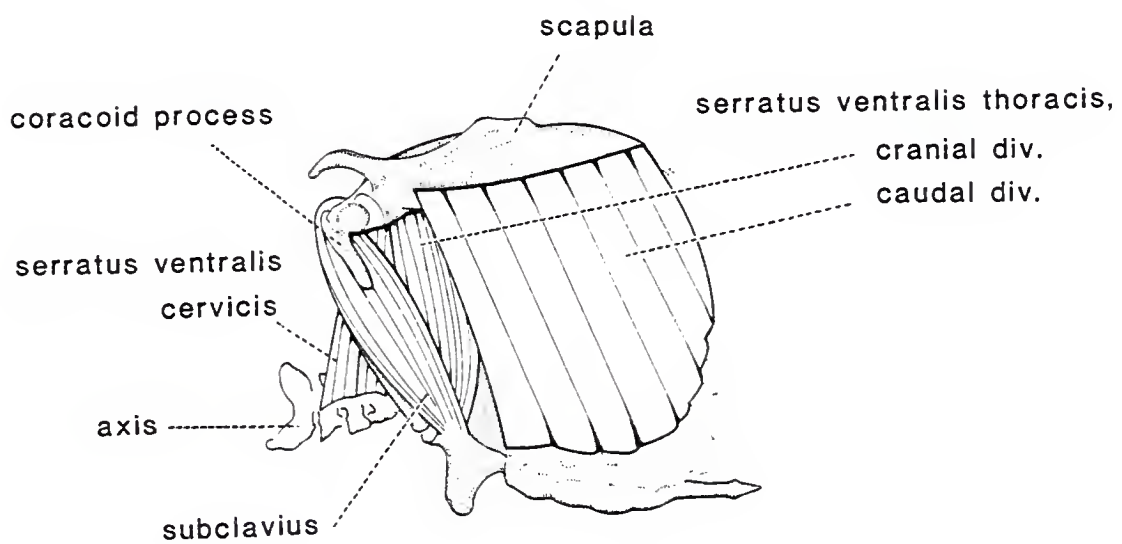
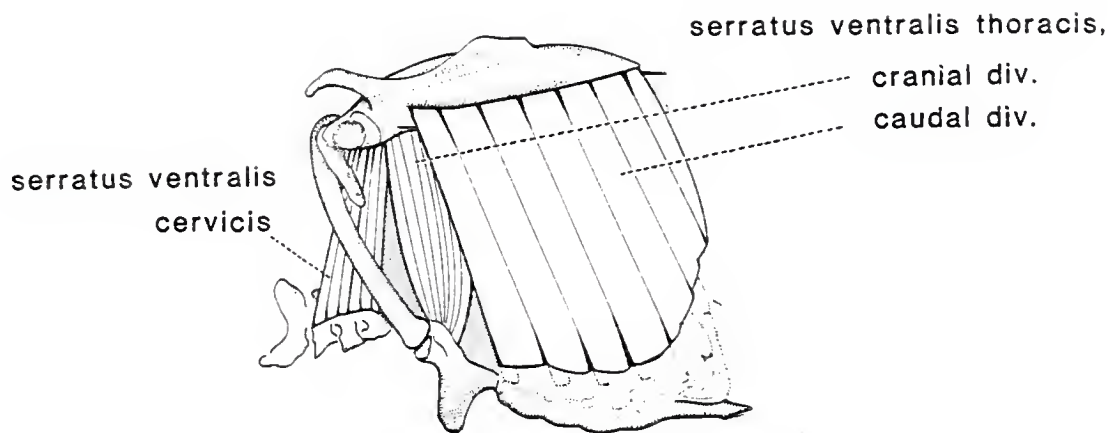
Serratus Ventralis Thoracis

Macalister (1872) observed and described the serratus magnus and divided the muscle into superior and inferior portions. The same muscle was described by Vaughan (1959) under the name serratus anterior. He also divided the serratus anterior into two parts, the anterior and posterior divisions. Subsequent authors followed his precedent for bats (Walton, 1967; Norberg, 1970; Strickler, 1978; Altenbach, 1979; Hermanson and Altenbach, 1981, 1983).

Serratus Ventralis Thoracis, Cranial Division

Form. The origin is a fibrous attachment on the dorsolateral surface of the first rib, first intercoastal space, and cranial surface of the second rib, medial to the origin of subclavius. The muscle has a broad fleshy insertion along the ventral surface of the craniomedial flange of the scapula, lateral to the insertion of serratus ventralis cervicis. At the origin, the belly is small and rounded. Distally the belly becomes wider and flatter, being thickest along the medial border. The muscle is innervated by a branch of the dorsal scapular nerve.

Figure 15.--Lateral view of serratus ventralis musculature. In the upper figure, subclavius is intact. In the lower figure, subclavius is removed to reveal the position of the deeper serratus ventralis cervicis.



Comparative aspects. The cranial division of serratus ventralis thoracis is large in hovering bats and in slow-flying bats (Strickler, 1978).

Functional aspects. Vaughan (1959) proposed that the cranial division functioned as a wing abductor by pulling ventrally on the craniomedial edge of the scapula. The cranial division is large in hovering bats, the glossophagines, and slow-flying bats, the rhinolophids (Strickler, 1978). In both groups, the wingbeat amplitude is large and may include extensive tipping of the lateral border of the scapula ventrad during the downstroke. The cranial division is situated to initiate abduction of the wing by arresting outward rotation and by initiating inward rotation of the scapula. No EMG data are available to test this hypothesis.

Serratus Ventralis Thoracis, Caudal Division

Form. The muscle originates by fibers along the dorsolateral aspect of ribs two through 11, adjacent and dorsal to each costochondral junction. A small, separate slip originates from the caudolateral aspect of the first costal cartilage, caudal to the origin of subclavius. The fibers of this small slip course caudally to insert on the middle one-third of the axillary border of the scapula. The fibers of the larger portion of the caudal division insert by fleshy attachment along the caudal three-quarters to seven-eighths of the axillary border and on the caudal angle of the scapula. The caudal fibers inserting upon the caudal angle constitute the thickest portion

of the muscle. Fibers are arranged in parallel. The fibers interdigitate at their origin with the scaleneus muscles cranially and the external abdominal oblique muscles caudally. Innervation of the caudal division is by the long thoracic nerve, coursing along the lateral surface of the muscle.

Comparative aspects. Strickler (1978) found that the caudal division is relatively large in most phyllostomids and small in the Pteropidae and most of the Verpertilionidae. He felt that the function and size of the muscle vary with respect to the development of the humeroscapular locking mechanism.

Functional aspects. The shoulder locking mechanism described by Vaughan (1959) provides a mechanical link between the action of the caudal division upon the scapula and the resultant adduction of the wing. Thus, contraction of the serratus ventralis thoracis was hypothesized to power the downstroke. Electromyograms obtained from Artibeus indicate that the posterior division has a major period of activity that commenced before onset of the downstroke and ended during the early downstroke. A second burst of activity is of shorter duration and occurs during the early upstroke phase. Hermanson and Altenbach (1981, 1983) reported a single period of activity for this muscle in Antrozous during the transition between the upstroke and downstroke. In both Antrozous and Artibeus, the pectoralis muscles are active prior to the major burst of the caudal division of serratus ventralis thoracis. The caudal division and pectoralis are coactive as adductors throughout the early downstroke.

The second period of EMG activity occurs after the upstroke has begun. This burst provides a force antagonistic to activity in clavodeltoideus and latissimus dorsi. Clavodeltoideus activity tends to protract the humerus, and thus advances the scapula cranial relative to the thorax. Latissimus dorsi exhibits its most pronounced activity as an abductor and pronator of the wing, causing retraction of the scapula and arm.

English (1978a, 1978b) presented data for the serratus ventralis cervicis and serratus ventralis thoracis of cats indicating biphasic activity patterns. He concluded that serratus ventralis thoracis is important in transmitting the weight of the body to the forelimbs during the stance phase, an observation suggested by earlier anatomists working only with cadaverous material (Davis, 1949; Gray, 1968). Of greater interest was English's observation that coactivation of cervical and thoracic portions of serratus ventralis during the swing phase effected shoulder extension and repositioning of the limb for the following step. Jenkins and Weijs (1979) found no significant difference between EMG activity of different slips of serratus ventralis thoracis in Didelphis. During walking, serratus ventralis of Didelphis was active during the propulsive phase. These authors commented upon a secondary period of activity during the swing phase in Didelphis, but did not discuss its role. A secondary phase of activity was not recorded in Antrozous (Hermanson and Altenbach, 1983). Repositioning of the limb for the downstroke may be effected in

Antrozous during the upstroke by the force of the airstream on the wing (Vaughan, 1959; Norberg, 1976) and by the action of the dorsal shoulder musculature (Hermanson and Altenbach, 1983). The greater wingloading in Artibeus may require an additional burst of muscle activity.

Rhomboideus

Form. The rhomboideus originates by fibers on the dorsal surface of the transverse process of cervical vertebrae seven, lateral to the cranial fibers of clavotrapezius, through thoracic vertebra six, lateral to the proximal fibers of acromiotrapezius. The muscle fibers course obliquely, caudodorsally through the interscapular region to insert on the entire vertebral border of the scapula caudal to the scapular spine. Innervation is by the dorsal scapular nerve.

Comparative aspects. The rhomboideus of the Phyllostomidae was characterized by Strickler (1978) as being relatively small. In contrast, both Macalister (1872) and Walton (1967) described the muscle as robust in the Phyllostomidae. I concur with Strickler's interpretation in part because of the muscle mass data presented in his arguments, whereas the other authors relied upon subjective interpretations. The romboideus is a thin, flat muscle in Artibeus. Strickler (1978) hypothesized that either rhomboideus or levator scapulae are well developed in bats depending on locomotor requirements. In the Molossidae, he observed that the rhomboideus was relatively large and adapted to rotating the caudal angle of the

scapula medially relative to an axis perpendicular to the dorsal surface of the scapula. He speculated that this action is important in terrestrial movements and not in the scapular movements associated with the phyllostomid shoulder during flight.

Functional aspects. Based upon the attachments and orientation, I deduce that rhomboideus pulls the caudal angle of the scapula ventromedially. There are no EMG data with which to elaborate upon this hypothesis.

Latissimus-subscapular Group

Latissimus dorsi

Form. The muscle originates from the superficial fascia overlying thoracic vertebra eleven through lumbar vertebra four. At the origin, the belly is thicker over thoracic vertebrae and grades into a thin aponeurosis caudally over the lumbar region. Latissimus dorsi inserts by a thin, 1 mm wide tendon 3-4 mm distal to the shoulder joint on the medial ridge of the humerus. The tendon lies ventral to and on the proximal edge of the fibrous insertion of teres major. Fibers in the latissimus dorsi are arranged in parallel at the origin, but converge distally on the tendon of insertion. Innervation is received from the thoracodorsal nerve.

Comparative aspects. Strickler (1978) did not observe much variation in the latissimus dorsi attachments of bats, except in the Rhinolophidae. In several phyllostomid species studied, the origin

of latissimus dorsi ranged between thoracic vertebra 10 and lumbar vertebra 5, but no correlation was established between the attachments and taxonomy or locomotor modes. Strickler's muscle mass data indicated that the muscle was largest in slow fliers, and average-sized in hovering and moderately fast frugivorous bats.

Functional aspects. The action of latissimus dorsi for Artibeus and for bats in general is confusing because of conflicting evidence from several sources. Latissimus dorsi was described by Vaughan (1959) as a pronator and flexor of the humerus, and also as an important retractor during terrestrial locomotion (1970b). Strickler (1978) added that the muscle might also serve in abduction of the wing during upstroke movements. For Desmodus, Altenbach (1978) obtained EMG data suggestive of a major role in humerus pronation and adduction, but not in abduction. In Antrozous latissimus dorsi functions primarily as a pronator during the downstroke (Hermanson and Altenbach, 1983).

The EMG data for latissimus dorsi in Artibeus are difficult to interpret in comparison with the data obtained from other studies. In 17 wingbeats, latissimus dorsi exhibits a biphasic activity pattern, with highest intensity EMG myopotentials observed during the late downstroke to early upstroke transition period (onset mean was 0.329, average onset of downstroke movements was 0.428). A second period of activity, of shorter duration and with lower amplitude myopotentials, occurs during the late upstroke and early downstroke. These patterns are consistent in all wingbeats. These data contrast with the EMG

pattern reported for Antrozous (Hermanson and Altenbach, 1983). Although the greatest activity for latissimus dorsi in Artibeus was observed during the late downstroke, the muscle was quiescent in Antrozous during the same period.

English (1978a) observed variability in the EMG patterns of latissimus dorsi in cats. Although the muscle was characterized by English as monophasic and active predominantly during the propulsive phase (E1-E2), he observed inconsistent bursts of activity during the swing phase (F). These inconsistent bursts are similar in timing to the late downstroke activity observed in Artibeus. Jenkins and Weijs (1979) reported monophasic activity in the posterior part of latissimus dorsi of walking Didelphis, however, they noted a consistent biphasic pattern for recordings made with electrodes located in the anterior fibers of the muscle. Placement of electrodes in intermediate positions resulted in "hybrid" EMG patterns: this region of latissimus dorsi was monophasic during some step cycles and biphasic during others. Tokuriki (1973a, 1973b, 1974) observed two distinct phases of activity in the latissimus dorsi of dogs at all gaits. One phase occurred with other flexor muscles during the F phase, contributing to lift the limb off the ground. A second and evidently more intense period of activity occurred throughout the propulsive phase. In terrestrial mammals, the activity of latissimus dorsi appears to be biphasic, although the most intense activity occurs during a different period of the locomotory cycle than observed in Artibeus.

Based on my EMG data and on comparative data for other mammals, I conclude that latissimus dorsi in both Artibeus and Antrozous stabilizes the shoulder and pronates the wing throughout the downstroke. Primary EMG activity occurs during the transition from downstroke to upstroke. Assuming a contraction time of 25 msec (Burke, 1978; Hermanson and Altenbach, 1981), the action of this muscle burst pronates the wing during the first third of the upstroke. Analysis of our film records indicates that the wing is continuously supinated during the first two-thirds of the upstroke (Norberg, 1976; Altenbach, 1978), an action effected by the dorsal abductor muscles and by the force of the airstream (Vaughan, 1959). The large burst of activity in latissimus dorsi may therefore be necessary to counteract the supinators and stabilize the shoulder during the early upstroke. The temporal activity pattern of latissimus dorsi indicates that the muscle is primarily a wing abductor.

Teres Major

Form. The teres major originates on the lateral and dorsal aspect of the caudal angle of the scapula, and along the caudal 3 mm of the axillary border of the scapula, by fibers. The origin does not extend to the cartilaginous expansion at the caudal angle of the scapula. The muscle inserts along the medial ridge of the humerus, 3-6 mm distal to the shoulder joint. The insertion is primarily a fibrous attachment, adjacent to but not conjoined with the tendon of insertion of the latissimus dorsi. All myofibers are arranged in parallel. Innervation is provided by several branches of the subscapular nerve.

Comparative aspects. Vaughan (1959) observed that the teres major in Macrotus (Phyllostomidae) is larger relative to the latissimus dorsi, than in Myotis (Vespertilionidae) and Eumops (Molossidae). Strickler (1978) found that both the teres major and latissimus dorsi exhibit positive allometry with respect to body mass. Triceps brachii (long head) and biceps brachii (short head) were the only other muscles in which Strickler observed positive allometry. He hypothesized that whereas musculoskeletal specializations or lift provided by the airstream permitted isometry to prevail in the primary adductors, and abductors, respectively, the muscles associated with powering the flick phase of the upstroke cannot be assisted by outside forces. Therefore, a greater degree of positive allometry is exhibited in these four muscles than in other muscles. Strickler did not include Artibeus in his sample but did study other phyllostomids, including Carollia and Phyllostomus, representative of locomotor styles broadly comparable to Artibeus.

Functional aspects. Electromyographic data exhibit two phases of activity. High-amplitude activity occurs during the late downstroke to upstroke transition. A second burst of one-half amplitude activity occurs during the late upstroke to downstroke transition. The association of muscle activity with turnover periods of the wingbeat cycle indicates these muscles play an important role in stabilizing the shoulder joint. Previous investigators used dissection studies and determined the role of teres major is responsible for pronation of the wing and a flexion of the shoulder joint (Vaughan, 1959; Norberg,

1970, 1972; Strickler, 1978; Altenbach, 1979). Hermanson and Altenbach (1983) reported EMG data for four wingbeats in Antrozous but made no specific conclusions beyond the classification of teres major as a bifunctional muscle. In Artibeus, the biphasic activity pattern is observed but is significantly different from that observed in Antrozous. The primary activity of teres major in Antrozous, during the final stages of the downstroke, probably pronates the wing synergistically with latissimus dorsi. Together, the two muscles counteract the onset of supination effected by the abductor muscles and airstream, and provide a smooth transition of wing movements between the downstroke and upstroke.

Subscapularis

Form. The subscapularis fills the entire subscapular fossa. The muscle originates along the periphery and on the elevated ridges of the subscapular fossa, and from the ventral surface of the cartilaginous expansion of the caudal angle of the scapula. The fibers exhibit a multipinnate arrangement, with two main tendons converging to the insertion on the lesser tuberosity of the humerus. The insertion is composed of a broad tendinous attachment, and by fibers coursing lateral of the tendon. Innervation is received from the two subscapular nerves, derived from the dorsal division of the brachial plexus.

Comparative aspects. The attachments of the subscapularis are conservative in all bats (Strickler, 1978). The large size of the

subscapularis relative to body mass was noted by Macalister (1872) as being largerr than observed in other mammals. Vaughan (1970a) elaborated upon this point and provided data for the mass of subscapularis relative to the total mass of the primary downstroke muscles. This value ranged from 16.1 to 19.4 percent. Overall, the relative weights of these primary downstroke muscles are consistent in all bats. The data from Strickler (1978) are in agreement with Vaughan except for in the Pteropodidae and for the phyllostomid genus Desmodus. Strickler commented that pteropodids were unique among bats in having small subscapularis muscles and small ventral muscle masses. It was not established whether the small muscle masses represent a primitive condition for chiropterans, or result from functional constraints. In contrast, the large subscapularis muscle of Desmodus appeared to be related to the terrestrial habits of the vampire bat, for which there are increased demands for shoulder extension and wing adduction (Strickler, 1978).

Functional aspects. Electromyography of the subscapularis in free-flying Artibeus indicates that the muscle remains active through approximately 75 percent of the wingbeat cycle. High-amplitude EMG activity is observed through approximately 26 percent of the wingbeat cycle and coincides with the second one-half of the upstroke and first one-tenth of the subsequent downstroke. This activity precedes myopotentials recorded from the other two downstroke muscles, serratus ventralis thoracis and pectoralis. Subscapularis was discussed as a

component of the rotator cuff complex of primates and other mammals (Tuttle and Basmajian, 1978) and is important in stabilizing the shoulder joint. This stabilization includes the role of holding the articular surface of the humerus within the glenoid fossa. Hermanson and Altenbach (1981, 1983) concluded that subscapularis was primarily responsible for fine control and stability of the shoulder joint in Antrozous. They also observed that the expression of continuous versus episodic activity in subscapularis was facultative and therefore dependent upon the nature of the flight maneuver being attempted at any given time. Kovtun and Moroz (1974) also used electromyography and observed that subscapularis preceded pectoralis activity and ceased activity 6-10 msec after myopotentials terminated in the "chest muscles" of Myotis myotis. It was not clear whether their data were pooled from several wingbeats or represented only one wingbeat.

The timing of subscapularis activity does not support Vaughan's hypothesis (1959) that subscapularis is the third muscle among the primary downstroke muscles to commence activity during a wingbeat. However, the high-amplitude activity fit well with the temporal pattern observed in downstroke muscles: myopotentials commence approximately 25 msec before wing adduction begins and terminates during the early downstroke. Low-amplitude myopotentials during the early downstroke and early upstroke indicate stabilization activity at the shoulder joint. Low-amplitude activity at the transition between downstroke and upstroke, and during the early upstroke stabilizes the shoulder against

forces produced by the abductor muscles during this period. Because of these two periods of activity and the roles that the muscle carries out, adduction and stabilization, the subscapularis is classified as a bifunctional muscle and serves primarily to stabilize the shoulder joint.

Deltoid Group

The deltoideus of bats has long been recognized as a tripartite muscle composed of three parts: clavodeltoideus, acromiodeltoideus, and spinodeltoideus (Macalister 1872). Because of functional specializations associated with each of these parts, I will describe and refer to each part specifically. All parts are innervated by the axillary nerve.

Clavodeltoideus

Form. The clavodeltoideus originates by fibers along the expanded, distal three-quarters of the clavicle. The muscle fibers course dorsally, proximal to the apex of the pectoral ridge of the humerus, and insert near the proximal insertion of acromiodeltoideus. Fibers are arranged in parallel.

Comparative aspects. Vaughan (1959) pointed out that the clavodeltoideus is separated from adjacent fibers of the pectoralis only with great difficulty. Visualization of the axillary nerve is necessary to correctly identify muscle bundles belonging to the

deltoideus group. Strickler (1978) illustrated some of the variation in extent of origin that is possible within the order Chiroptera and thus the need to undertake careful dissection of this region.

Functional aspects. The functional analysis of clavodeltoideus is discussed along with the spinodeltoideus.

Acromiodeltoideus

Form. The acromiodeltoideus has a fibrous origin along the entire tip of the acromion process and proximally, along the base of the acromion process as it intergrades with the scapular spine. Insertion is by fibrous attachment along the lateral ridge of the humerus, from 1 mm distal to the greater tubercle along the proximal one-third of the humerus. The myofiber architecture is parallel with some fibers diverging distally along the insertion. A thin fascial plane bisects the muscle into anterior and posterior portions and extends distally from the middle of the acromion process.

Comparative aspects. The primitive condition for the origin of the chiropteran acromiodeltoideus is restricted to the acromion process (Strickler, 1978). In advanced families, the origin of the muscles has extended medially along the scapular spine, a position that places fibers farther from the shoulder joint and that increases the effectiveness of acromiodeltoideus as an abductor and flexor of the shoulder (Strickler, 1978). In Antrozous, fibers of acromiodeltoideus and acromiotrapezius attach to each other along the dorsal scapular

ligament (Hermanson, 1978). The situation in Artibeus, in contrast, is for both acromiodeltoideus and acromiotrapezius to insert upon a solid mass of bone, adjacent to the acromion process.

Functional aspects. The action of the acromiodeltoideus is discussed along with the spinodeltoideus.

Spinodeltoideus

Form. The spinodeltoideus originates by fibers from the dorsal scapular ligament (sensu Hermanson and Altenbach, 1983), from the vertebral border of the scapula caudal to the scapular spine, and over the cartilaginous plate at the caudal angle of the scapula. Insertion is by an aponeurosis on the medial aspect of the dorsal ridge of the humerus, deep to the insertion of the acromiodeltoideus and immediately distal to the insertion of teres minor. The muscle is parallel-fibered and forms a broad but thin sheet over the caudal scapular region. Vaughan (1959) commented that spinodeltoideus was composed of two parts in Macrotus.

Functional aspects. The deltoideus muscle of man is a single muscle mass that was divided by anatomists into an anterior and posterior portion. Each division can be correlated with differential EMG activity while performing several actions (Inman et al., 1944). Similarly, Hermanson and Altenbach (1983) presented functional interpretations for all three heads in Antrozous and discussed these data with respect to published data for several terrestrial mammals. The acromiodeltoideus and spinodeltoideus EMG patterns for Antrozous

were in general agreement with the hypotheses of earlier descriptive studies (Vaughan, 1959, Strickler, 1978): the muscles functioned as abductors of the wing. The clavodeltoideus, however, was active almost in synchrony with the primary downstroke muscles. This observation, and dissection studies (Norberg, 1972; Strickler, 1978), led Hermanson and Altenbach to conclude that the muscle was an important humeral protractor and also a humeral adductor.

During the propulsive phase in Antrozous, a lack of muscle activity in acromiodeltoideus and spinodeltoideus contrasted with observations of EMG patterns in the deltoideus of terrestrial mammals. Deltoideus activity occurred during the stance phase in stepping cats at several speeds of locomotion (English, 1978a). Biphasic activity occurred in the deltoideus muscle in Didelphis: the largest amplitude activity occurred during the swing phase, and a less intense period of activity during the stance phase (Jenkins and Weijs, 1979). When the acromioclavicular and spinal portions of the Didelphis deltoideus were monitored simultaneously, the spinal portion exhibited intense activity during the first one-third of the swing phase, while the acromioclavicular portion was active during the final two-thirds of the swing phase (Jenkins and Weijs, 1979). Recordings from the deltoideus of Canis indicated continuous myopotentials throughout the step cycle of walking, trotting, and galloping dogs (Tokuriki, 1973a, 1973b, 1974).

Data for the deltoideus of Artibeus provide contrasts and similarities with the Antrozous observations. For example, the primary (highest amplitude) EMG activity in the clavodeltoideus was evident during the downstroke portion of the wingbeat. Myopotentials commenced almost in synchrony with the pectoralis, contributing to wing adduction but also to the anterior movement of the wing. This wing protraction is an important aspect of the "Rudderflug" or rowing flight described by Eisentraut (1936) and Norberg (1976). Low-amplitude activity of brief duration occurs during the transition between downstroke and upstroke and serves to stabilize the scapula. In contrast, highest-amplitude activity in both the acromiodeltoideus and spinodeltoideus occurred during the late downstroke and early upstroke. These data therefore suggest an important role for acromiodeltoideus and spinodeltoideus in wing abduction and agree with observations in Antrozous (Hermanson and Altenbach, 1983). Both acromiodeltoideus and spinodeltoideus were biphasically active. The posterior part of acromiodeltoideus showed a low-amplitude phase of activity roughly coincident with the primary burst of clavodeltoideus, although of shorter duration and with less amplitude than in the latter muscle. Spinodeltoideus exhibited low-amplitude activity during the first one-third of the downstroke. These secondary EMG bursts in the acromiodeltoideus and spinodeltoideus may stabilize the shoulder against the powerful actions of the pectoralis.

Suprascapular Group

Supraspinatus

Form. Supraspinatus originates by fibers along the cranial and medial perimeter of the supraspinous fossa, deep to the belly of acromiotrapezius. The muscle fibers are arranged in parallel. This muscle has a fibrous insertion on the tip of the greater tubercle of the humerus. Innervation is by the suprascapular nerve.

Comparative aspects. The supraspinatus exhibits little variation in its attachments for all bat species (Vaughan, 1959, 1970a; Strickler, 1978). The regression of supraspinatus mass against body mass suggests that the size of this muscle is average to relatively large size in slow-flying bats, and smaller in faster-flying species (Strickler, 1978).

Functional aspects. The mammalian supraspinatus is considered one of the rotator cuff muscles of the shoulder: its primary role is to stabilize the glenohumeral articulation in concert with the infraspinatus, subscapularis, and teres minor (Hollinshead, 1974; Tuttle and Basmajian, 1978). For bats, Vaughan (1959) described the general action of the supraspinatus to be shoulder extension and humerus supination, a description accepted by subsequent authors (cf. Strickler, 1978). Vaughan (1959) suspected that supraspinatus was most effective as a shoulder extensor in the phyllostomid Macrotus, as compared to Eumops and Myotis. The shoulder joint of Macrotus allows

more freedom of movement than is observed in Eumops and Myotis. Both of the latter species had bony locking mechanisms that restricted movement of the humerus in both the dorsoventral and craniocaudal directions. Thus, the humerus of Macrotus could be extended cranial to a transverse plane through the shoulder, while the humerus of Eumops could only be extended forward to this plane.

Electromyographic data for the supraspinatus is available for only six wingbeats, primarily because the small size and deep position of the muscle make the surgical implantation a traumatic procedure for the animal. The muscle exhibited a single, extended period of activity commencing during the early upstroke, and continuing through the early downstroke. During two of the wingbeats, supraspinatus exhibited two periods of normal-amplitude EMG activity with a brief period of quiescence interposed.

Biphasic EMG activity was observed in supraspinatus of Antrozous (Hermanson and Altenbach, 1983). Biphasic activity was also observed during the step cycle of Didelphis (Jenkins and Weijs, 1978), but not during stepping in cats (English, 1978a) or dogs (Tokuriki, 1973a, 1973b, 1974). In several primate species, Tuttle and Basmajian (1978) reported prominent activity of the supraspinatus during humeral elevation and cautioned that the function of this muscle may be one of acceleration of the humerus rather than as a simple stabilizer (i.e., rotator cuff). The variability observed in all of these studies may be attributed to small sample sizes, at least for the two bat species

studied, and to an inconsistent pattern of locomotor movements studied in the primate examples. In the latter study, movements of the animal were not restricted to forward progression, but instead included forward, lateral, and vertical movements. Support for a role in wing supination is provided by EMG data indicating activity during the early upstroke when the wing is supinated and abducted.

Infraspinatus

Form. The infraspinatus originates from the periphery of the infraspinous fossa of the scapula: cranially from the spine of the scapula; medially from the dorsum of the vertebral border of the scapula; and laterally from the raised ridge of the infraspinous fossa. All fibers insert upon a central tendon that courses through the middle of the muscle. This tendon forms the sole insertion of the infraspinatus upon the lateral ridge of the humerus. Fibers at the medial end (nearest the vertebral border) are the longest in the muscle and insert upon the central tendon at an acute angle. Fibers that insert more distally on the central tendon are shorter and tend to intersect the tendon at a larger angle than the medial fibers.

Innervation is by the suprascapular nerve, after that nerve provides a branch to the supraspinatus and courses laterally under the tip of the acromion process.

Comparative aspects. Strickler (1978) noted little variation in the attachments of the infraspinatus in all bat species that he studied. In contrast to the regression of muscle mass on body mass

obtained for supraspinatus, Strickler observed that the muscle was larger in fast-flying species, but smaller in fast-flying frugivores. No functional explanation was provided. Within families, there was no consistent ratio observed between the mass of infraspinatus and supraspinatus.

Functional aspects. Two phases of activity were evident in the infraspinatus of Artibeus. The first period and the one exhibiting the highest amplitude myopotentials commenced immediately prior to the onset of downstroke movements, and continued during the first third of the downstroke. A second, less intense period of activity was observed in six wingbeats during the late downstroke and early upstroke. These data were similar to observations made on the infraspinatus of Antrozous (Hermanson and Altenbach, 1983). Although two distinct phases were also observed in walking Didelphis (Jenkins and Weijs, 1979), only one period of activity was noted in cats (English, 1978) and dogs (Tokuriki, 1973a, 1973b, 1974) at all gaits.

On the basis of anatomical position the infraspinatus is a shoulder flexor, and a humerus abductor and supinator (Hermanson and Altenbach, 1983; Strickler, 1978; Altenbach, 1979). The biphasic activity pattern suggests an underlying stabilizing role at the shoulder; the secondary EMG activity observed during the early downstroke counteracts the action of the pectoralis and protects the glenohumeral joint in association with other intrinsic muscles of the shoulder. Because the wing of a bat is not capable of being

"feathered" during the upstroke like that of a bird, the role of the abductors is accentuated in bats (Vaughan, 1959). Thus, the *infraspinatus* exhibits strong activity during the non-propulsive upstroke, and acts in concert with the more superficial *spinodeltoideus* to abduct the wing.

Triceps Group

The triceps brachii is composed of three heads in most mammals. Each head is innervated by branches of the radial nerve. Because of the different origins of these heads, each is treated separately.

Triceps Brachii, Medial Head

Form. The medial head has a fleshy origin along the caudal surface of the humerus, approximately 10-13 mm distal to the greater tubercle. Muscle fibers pass medial to the radial nerve. Fibers insert distally in a unipinnate fashion on the main triceps brachii tendon. This is the smallest of the three heads of triceps brachii.

Comparative aspects. In most phyllostomids, the medial head originates on the middle one-third of the ventral surface of the humerus (Strickler, 1978). The attachments are conservative in most chiropterans.

Functional aspects. The medial head of triceps brachii spans one joint, the elbow. Vaughan (1959) suggested that the medial head stabilizes the sesamoid bones found at the insertion of the triceps brachii tendons in many bats. No EMG data are available for any bats to corroborate or refute the hypothesis.

Triceps Brachii, Lateral Head

Form. The lateral head originates by fibers on the proximal one-quarter of the humerus, primarily on the caudal surface adjacent to the greater tubercle, surgical neck, and lesser tubercle. All fibers pass lateral to the radial nerve. Central fibers insert directly upon a central tendon of insertion. Peripheral fibers insert on either side of this tendon at an angle of less than 10 degrees.

Functional aspects. The lateral head of triceps brachii crosses one joint, the elbow joint, and is capable to effecting extension of that joint. EMG data is discussed along with the long head of triceps brachii.

Triceps Brachii, Long Head

Form. The long head arises from the axillary border of the scapula, adjacent to the infraglenoid tubercle. The muscle is pinnate. Fibers course distally to insert upon a central tendon in common with the other two heads of triceps brachii. The main insertional tendon contains a small sesamoid caudal to the elbow joint. A synovial cavity is present deep to the tendon, permitting movement of the tendon relative to the joint in this area. The insertional tendon of the triceps brachii attaches to the caudal surface of the olecranon region of the ulna.

Comparative aspects. The anatomy of the triceps brachii does not depart significantly from the general pattern observed in other bats (cf. Strickler, 1978): the long head spans the shoulder and elbow joints, the lateral head spans only the elbow joint.

Functional aspects. In terrestrial mammals, the triceps brachii function as anti-gravity muscles principally by maintaining elbow extension during standing or locomotion (Armstrong et al., 1982; English, 1978b; Jenkins and Weijs, 1979). EMG data for long and lateral head of triceps brachii in Antrozous did not clearly support an elbow extensor hypothesis (Hermanson and Altenbach, 1983). In A. jamaicensis, muscle activity in the long head commenced prior to initiation of the upstroke, and continued throughout the first one-half of the upstroke. The lateral head also commenced activity prior to the downstroke, but relative to the long head, EMG activity began later and was of shorter duration. These temporal patterns are similar to observations of triceps brachii activity in Antrozous (Hermanson and Altenbach, 1983). In both bat species, the long and lateral heads of triceps brachii exhibited activity patterns associated with wing abduction. It is not clear how either portion of triceps brachii effects elbow extension, a movement associated with the downstroke phase of the wingbeat cycle (Eisentraut, 1936; Norberg, 1976; Hermanson and Altenbach, 1983). Elbow extension automatically contributes to spreading the distal wing during the downstroke in many bat species (Vaughan, 1966; Vaughan and Bateman, 1970). In Artibeus, the amount of time between EMG onset and downstroke initiation was approximately 55 msec. Armstrong et al. (1977) and Hermanson and Foehring (1982) demonstrated the existence of fast type histochemical profiles for triceps brachii in Myotis and Tadarida, respectively. In several mammalian muscles, fast type profiles are correlated with contraction

times of less than 35 msec (Burke, 1978). The effect of activity in triceps brachii is implemented during the upstroke, at first to abduct the limb, and then possibly during the late upstroke, to extend the elbow.

Pectoralis Group

Subclavius

Form. The subclavius originates along the lateral aspect of rib one and the associated costal cartilage by fibrous attachments. The muscle inserts on the distal seven-eighths of the ventrolateral surface of the clavicle, by fibers. The muscle exhibits a parallel-fiber architecture. Innervation is received from the upper pectoral nerves.

Comparative aspects. The attachments of the subclavius are relatively similar in all bats with most differences limited to the position of the insertion upon the clavicle (Strickler, 1978). Struhsaker (1963) reported that the subclavius is relatively larger in bats that have low aspect ratio wings. Altenbach (1979) noted the robust nature of the subclavius in Desmodus, particularly with respect to the insertion of the muscle upon nine-tenths of the length of the clavicle. In Desmodus the ability to adduct the limb rapidly and shoulder girdle is important in avoiding injury or predation. The former situation could accrue while the vampire bat approaches the

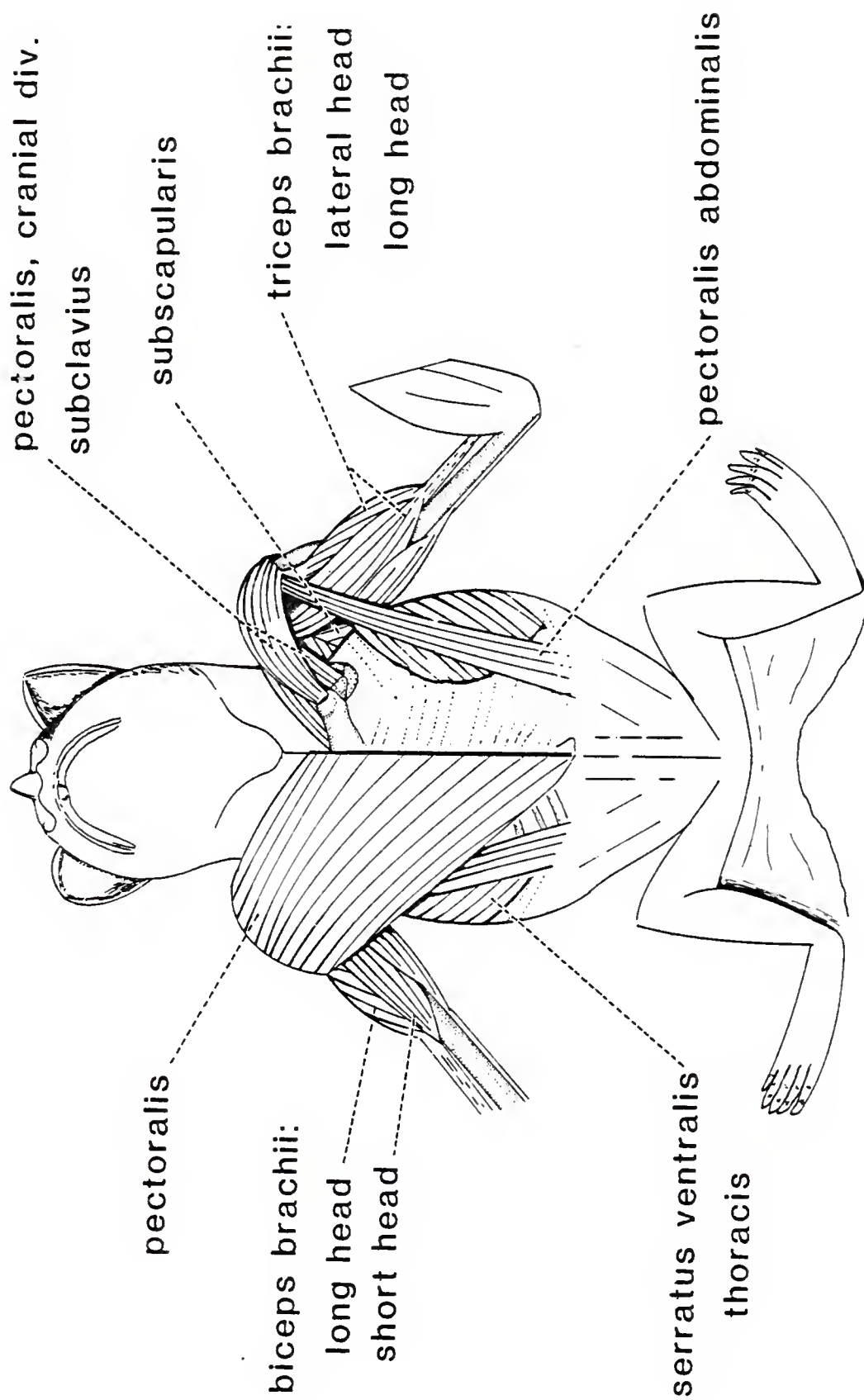
fetlock joint of livestock and the potential predator steps back suddenly or kicks at the bat. Also, lift off from the ground after feeding is complicated by the added weight of the blood meal. Altenbach (1979) felt that the subclavius, through its action on the clavicle, could power the initial leap off the ground into flight.

Functional aspects. Vaughan (1959) deduced that the subclavius pulls the clavicle ventrally and caudally, probably to steady the clavicle against the forces of the dorsal abductor muscles. This movement of the clavicle has been construed to contribute to wing adduction in two ways. As previously mentioned, the clavicle may adduct in synchrony with the wing during initial take-off maneuvers. Also, adduction of the clavicle in synchrony with the wingbeat contributes to effective force production in the major downstroke muscle, the pectoralis, by reducing the overall excursion that this latter goes through during the downstroke (Hermanson, 1981).

Pectoralis

The pectoralis muscle is divided into two parts in all bats (Strickler, 1978), although the division is not usually visible on the superficial surface of the muscle. The cranial division (clavicular head) arises from the clavicle and parts of the manubrium. The caudal division (sternal portion) arises from the sternum inclusive of parts of the manubrium and the xiphoid process.

Figure 16.--Ventral view of the shoulder and arm of Artibeus jamaicensis.
Superficial muscles are exposed on the left; deeper muscles are exposed
on the right.



In many terrestrial mammals, the pectoralis includes a transverse head located cranially and superficially, and a deep head originating more caudally and coursing deep to the transverse head (Howell, 1926; Rinker, 1954; Getty, 1975). The cranial division is equivalent to the anterior division of Vaughan's terminology (1959) and in bats may be homologous to the transverse pectoralis of other mammals. The caudal division is equivalent to the posterior division of Vaughan's terminology. However, the variation observed within the chiropteran pectoralis makes it difficult to consistently delineate the two divisions. The pectoralis minor of humans and other higher primates cannot be related with either part of the chiropteran pectoralis complex (cf. Inman et al., 1944). I follow Vaughan's descriptions of the myology of pectoralis, but have changed the terminology to avoid the use of the terms "anterior" and "posterior," in accordance with usage prescribed in the N.A.V.

Pectoralis, Cranial Division

Form. The cranial division of pectoralis arises from the cranial end of the manubrium, and from the proximal two-thirds of the ventral surface of the clavicle, by fibers. The insertion is by fibers along the ridge extending from the greater tubercle to the pectoral ridge and along the apex of the pectoral ridge superficial to the insertion of the caudal division of this muscle. Innervation is by the cranial pectoral nerves. The muscle fibers are parallel-fibered.

Comparative aspects. The cranial division is difficult to separate from the adjacent clavodeltoideus in phyllostomids. Consequently, Strickler (1978) combined the two muscles for the purposes of description. Strickler reported that the combined relative mass of the cranial division and the clavodeltoideus was large in phyllostomid bats and particularly large in hovering species.

Functional aspects. The cranial division is discussed along with the functional aspects of the caudal division of pectoralis.

Pectoralis, Caudal Division

Form. The caudal division of pectoralis arises by fibers along the entire sternum from the keeled ventral portion of the manubrium, from a raphe ventral to the mesosternum, and by fibers from the ventral surface of the xiphisternum. Some deep fibers have a fleshy origin from the ventral aspects of costal cartilages 2-4 and intercostal spaces 2-3. At the caudal end of the muscle, some laterally placed fibers attach to the abdominal fascia, ventral to the costal arch. Fibers are generally arranged in parallel but converge laterally. The insertion is both fibrous and aponeurotic along the distal one-half of the pectoral ridge and along the cranial face of the humerus, 3 mm distal to the pectoral ridge, distal to the insertion of pectoralis abdominis, and cranially, deep to the insertion of the cranial division of pectoralis.

Comparative aspects. The caudal division of pectoralis attains its greatest relative size in the pteropodids and in Nycteris. In these bats the caudal division of serratus ventralis thoracis is not

well developed to assist the pectoralis as an adductor of the scapula (Strickler, 1978). Otherwise, the form of the muscle is conservative among all bats (Vaughan, 1970a; Strickler, 1978).

Functional aspects. The pectoralis muscle of Artibeus was analyzed in six regions to determine whether the muscle exhibits homogeneous activity patterns. The origin extends along the entire sternum, with fibers at the cranial end coursing at an angle of approximately 60 degrees relative to the median plane, and caudal fibers coursing approximately 40 degrees relative to the median plane. Vaughan (1959) concluded that different regions of the muscle were important in terms of the cranial or caudal components of force that were exerted upon the humerus. In an analogous muscle, Herring et al. (1977) demonstrated that different regions of the masseter muscle of miniature pigs were active at different points in the chewing cycle, a pattern they labelled functional heterogeneity. The pectoralis of bats is similar in that the muscle is broad along the origin, with fibers converging distally upon the insertion. Electromyograms in the pectoralis of Artibeus exhibit a general gradient of activity: muscle activity occurred earliest in cranial bundles of the muscle, the cranial division. There was not a sequential cranial to caudal sequence of EMG onset in regions 1-5 (see Figure 17 for identification of electrode locations). Region 3, the middle of pectoralis was active next, followed in order by Regions 2, 1, 5, and 4. Based upon the similarity in mean onset times, it is not possible to assess

Figure 17.--Electromyographic data for six regions in the pectoralis muscle during slow flight. Electrode locations are indicated in the upper figure, a ventral view of Artibeus jamaicensis. Position 1 is in the cranial division of pectoralis. Positions 2 to 6 are in successively more caudal locations of the caudal division of pectoralis. In the lower figure, unshaded bars indicate observed periods of normal-amplitude muscle activity. Vertical lines are placed one standard deviation from the means of activity onset and termination.

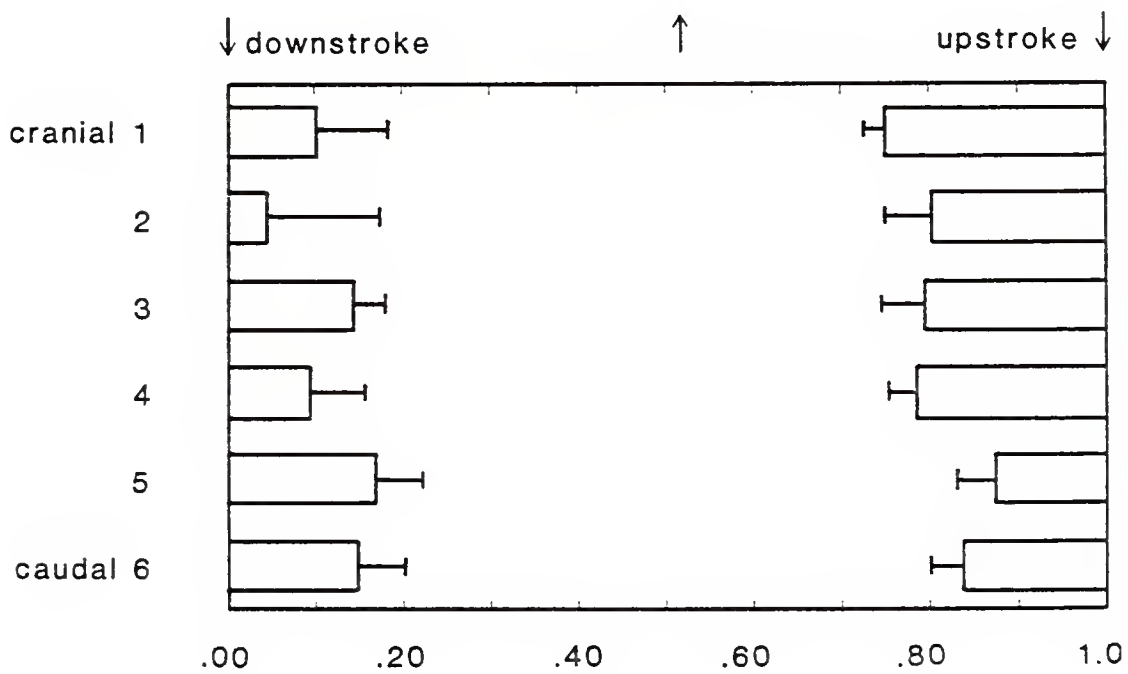
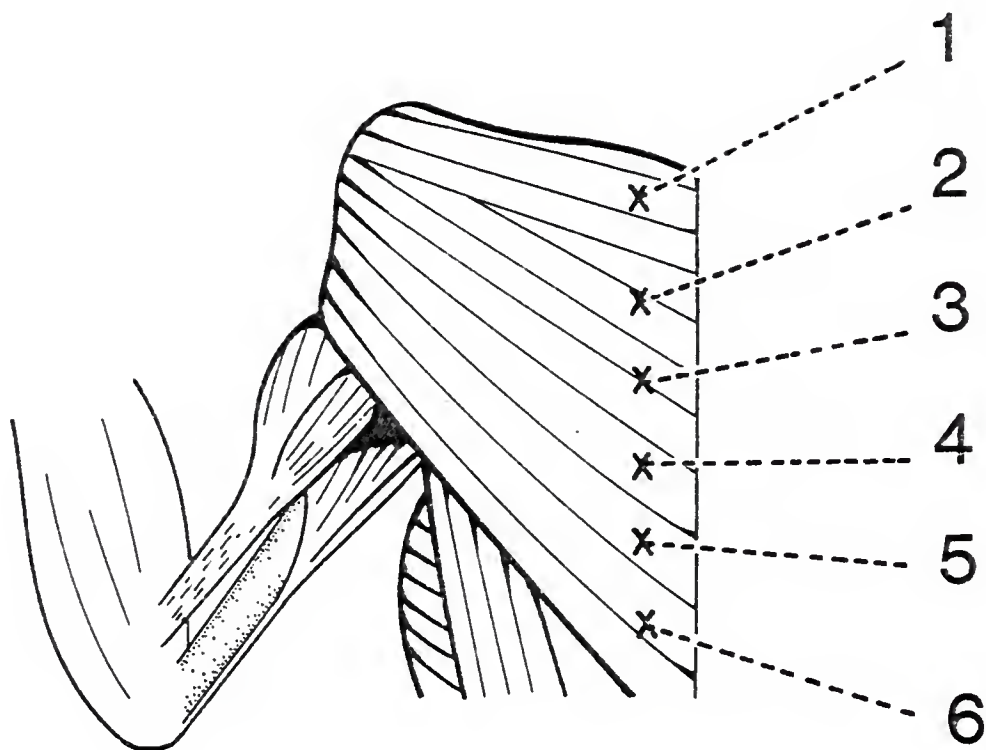


Table 3.--Electromyographic data for activity patterns in six regions of the pectoralis muscle of Artibeus jamaicensis during slow flight. N= number of wingbeats analyzed per muscle. Mean duration of the downstroke and time of muscle activity onset and termination are expressed as a numerical value relative to the total wingbeat cycle (mean \pm one S.D.).

		N	Downstroke Duration	Onset Time (S.D.)	Termination Time (S.D.)
Cranial division	1	12	0.494	0.749 (.022)	0.105 (.080)
Caudal division	2	9	0.533	0.801 (.048)	0.045 (.135)
	3	17	0.496	0.792 (.050)	0.145 (.034)
	4	7	0.526	0.785 (.031)	0.094 (.086)
	5	9	0.526	0.877 (.039)	0.170 (.056)
	6	7	0.542	0.837 (.036)	0.149 (.054)

activity heterogeneity within the pectoralis. A better determination should be made with simultaneous recordings from all six regions in one bat. In order to perform this experiment, a sufficiently light electrode and plug assembly must be designed for use in bats.

The EMG data obtained for Artibeus corresponds with data for Antrozous (Hermanson and Altenbach, 1981, 1983) and Eptesicus (Altenbach and Hermanson, unpublished). A single phase of activity began during the late upstroke and continued through the early downstroke of the following wingbeat. Hermanson and Altenbach (1981) suggested that pectoralis is the primary muscle powering the downstroke of bats. Because of the high frequency and short duration of the chiropteran wingbeat, the pectoralis exhibits electrical activity during the late upstroke. The mechanical effect of the myopotential is not realized until the transition from upstroke to downstroke. There is a 22-25 msec delay between the onset of pectoralis activity and the beginning of the downstroke. Mechanical studies of other mammalian muscles demonstrated that a 25 msec delay between onset of EMG activity and maximum tension production is expected during isometric contractions of fast twitch muscles (Burke et al., 1974; Burke, 1978). Chiropteran pectoralis muscle has been classified as fast twitch using several histochemical staining techniques (Armstrong et al., 1977; Hermanson and Foehring, 1982). Activity in the pectoralis terminates during the first one-third of the downstroke. The muscle remains quiet during the remainder of the wingbeat cycle.

Electromyograms obtained from stepping opossums (Jenkins and Weijs, 1979) and cats (English, 1978a) indicated that pectoralis in terrestrial mammals was active throughout relatively more of the propulsive phase than in bats. In the present study, the propulsive phase of terrestrial stepping is considered to be equivalent to the downstroke of flying bats.

Pectoralis Abdominalis

Form. Pectoralis abdominalis lies deep to the pectoralis. The origin of this muscle is along the ventral surface of the costal arch and on the surface of the external abdominal oblique muscles, extending from 7-12 mm lateral of the median plane. Insertion is by a flat tendon on the ventral, medial surface of the humerus, proximal to the apex of the pectoral ridges.

Comparative aspects. The pectoralis abdominalis has been described in bats (Strickler, 1978) and rodents (Woods, 1972). The muscle does not occur in domestic mammals (Getty, 1975; Evans and Christensen, 1979). Macalister (1872) doubted synonymy with the "lesser pectoral or pectoralis minor" of man because the pectoralis abdominalis is innervated by the anterior thoracic nerve from the "outer cord of the brachial plexus, not by the middle, which should supply it if it were the lesser pectoral." The muscle was similar in all chiropterans (Strickler, 1978).

Functional aspects. Vaughan (1959) concluded that the muscle was not important in flight. He noted that it was best developed in bats using extensive terrestrial locomotion in their locomotor repertoire.

The muscle was also well developed in Antrozous (Hermanson, 1978) and Desmodus (Altenbach, 1979). Both of these bats feed upon items located on the ground.

Flexor Group of Arm

Coracobrachialis

Form. The coracobrachialis muscle is small and unipinnate, arising from the lateral tip of the coracoid process deep to the short head (coracoid head) of biceps brachii. Insertion is by a single tendon on the anterior surface of the shaft of the humerus, approximately two-thirds of the distance along the humerus. Fibers insert along the tendon at an angle of approximately 18-22 degrees.

Comparative aspects. The muscle belly is small relative to the adjacent long and short heads of biceps brachii (Strickler, 1978). The coracobrachialis is not present in the Molossidae (Vaughan, 1959, 1970b). Innervation is by a proximal branch of the musculocutaneous nerve.

Functional aspects. The function of coracobrachialis was described by Vaughan (1959), Altenbach (1979), and Strickler (1978) as a weak adductor of the wing. No EMG data are available for this muscle.

Biceps Brachii

Synonymy. The biceps brachii includes two heads in bats. Vaughan (1959) introduced the terms "coracoid head" and "glenoid head" to parallel the "short" and "long" terminology used in human anatomy. I

will use the latter terms in accordance with usage proposed in the N.A.V. Both heads are innervated by the musculocutaneous nerve after the nerve emerges through the lateral surface of coracobrachialis.

Form. The long head of biceps brachii originates from the lateral surface of the base of the coracoid process by a stout tendon. The tendon courses laterally across the shoulder joint capsule and emerges through the bicipital groove, ventral to the pectoral ridge. Fibers attach to the tendon or origin in a fusiform pattern but are generally arranged in parallel throughout the belly. Distally, the fibers attach to a broad tendinous sheet that narrows distally and courses to the flexor groove on the anterior surface of the radius.

The short head of biceps brachii originates from the ventral tip of the coracoid process. The fibers are arranged in parallel. Distally, the fibers converge on a single tendon that inserts on the flexor groove of the radius, separate from and proximal to the insertional tendon of the long head.

Functional aspects. Although no EMG data is available for the biceps brachii of A. jamaicensis, the anatomy of the muscle and its two heads is sufficiently similar to the condition in Antrozous to permit some comparison. Hermanson and Altenbach (1983) noted biphasic activity patterns in both the long and short heads of biceps brachii. These authors concluded that the long head initiated elbow flexion during the upstroke. Later during the upstroke, a burst of activity

in the short head contributed to elbow flexion. Electromyograms also demonstrated muscle activity throughout middle and later portions of the downstroke in the short head, preceded by a burst of activity during the early downstroke in the long head. Therefore, both heads of biceps contributed to wing adduction, and also to elbow flexion.

Brachialis

Form. The brachialis is a small muscle located on the lateral aspect of the arm. The origin is fleshy, along the dorsolateral surface of the humerus and along the middle one-third of that bone. Fibers of brachialis insert along the anterior surface of the radius, proximal to the insertion of biceps brachii. The radial nerve courses alongside the muscle in the arm, however, the innervation of brachialis is by fibers of the musculocutaneous nerve.

Functional aspects. Although brachialis is an important elbow flexor in most mammals (observation based on its one-joint condition), it is weak and probably ineffectual in Artibeus and in other bats.

Antebrachial Extensor Group

The forearm muscles of the chiropteran wing include those muscles originating on the distal end of the humerus and extending to insert upon the antebrachial bones, the manus, and on the digits. These muscles are small and difficult to see, precluding a thorough

comparative discussion. However, a description of their anatomy and proposed function in Artibeus is included here.

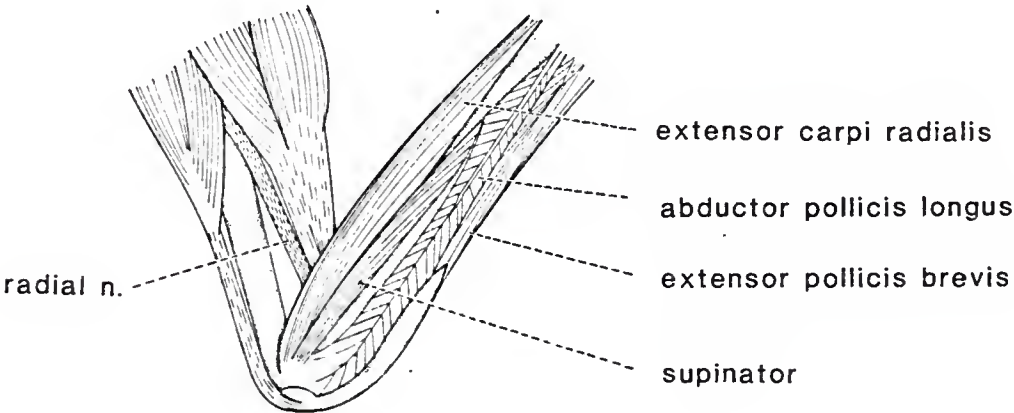
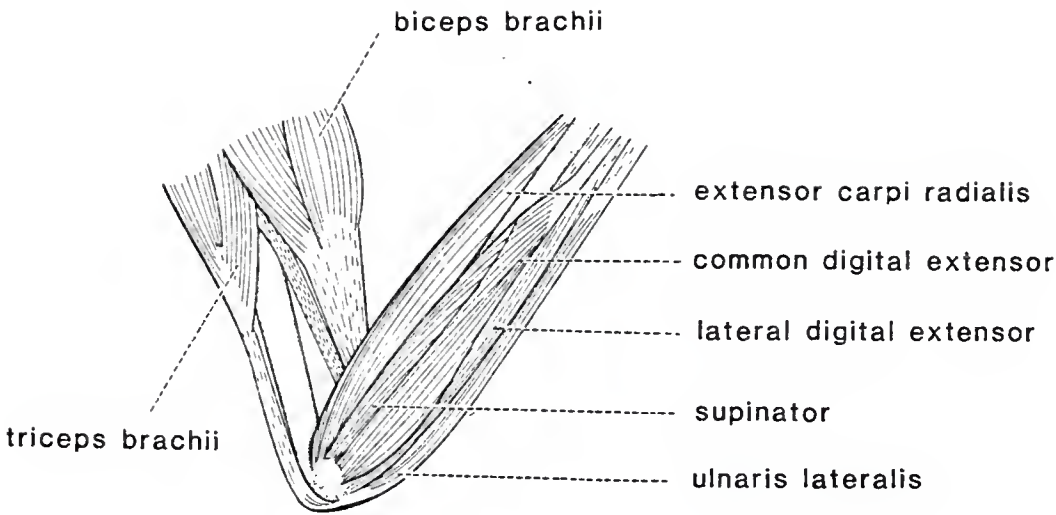
The forearm muscles include a superficial group that originate near or upon the lateral and medial epicondyles of the humerus. Although these muscles probably stabilize the elbow joint, their function is of greatest importance at the wrist or digital joints. At the elbow joint, the brachial (triceps brachii and biceps brachii) possess the greatest mechanical advantages and are primarily responsible for elbow flexion and extension. The deep layer of forearm muscles originate in general from the radius, ulna, or interosseus membrane. These muscles produce wrist or digital movements. The following descriptions provide a foundation for future studies of the forelimb musculature in Artibeus and in other bats.

Extensor Carpi Radialis

The extensor carpi radialis is usually treated as two separate muscles (cf. Rinker, 1954; Vaughan, 1959). I discuss the two heads as a single functional unit both for simplicity and because the bellies and proximal tendons are separable only with great difficulty in Artibeus.

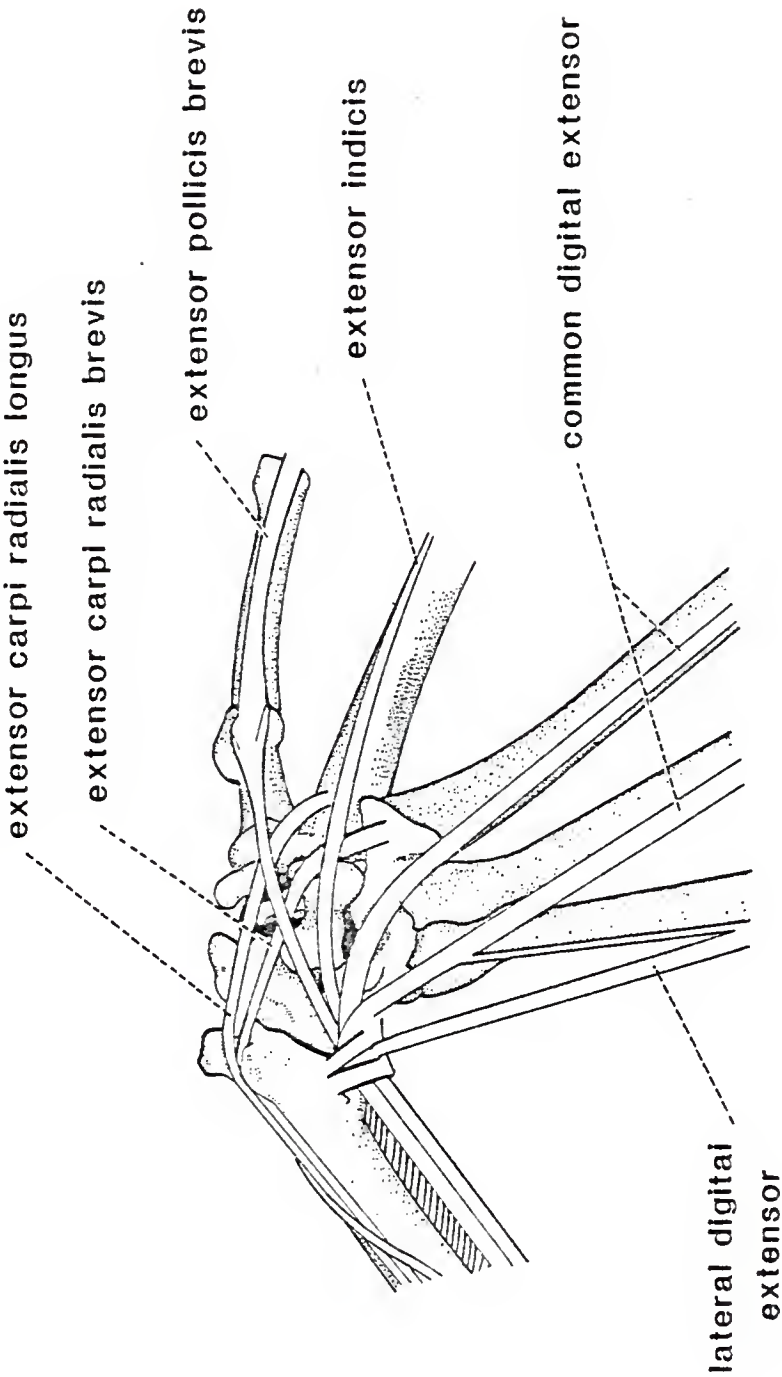
Form. The extensor carpi radialis longus has a tendinous origin on the caudal surface of the epicondylar ridge. A small number of fibers sweep proximally from this tendon along the epicondylar ridge. Insertion is on the dorsal base of metacarpal I and on the

Figure 18.--Lateral view of the muscles of the elbow region. The upper figure demonstrates the superficial muscles. Deeper muscles are exposed in the lower figure by removal of the common digital extensor and ulnaris lateralis.



5 mm

Figure 19.--Dorsal view of the muscles of the carpal region. The intrinsic muscles of the manus have been removed.



5 mm

anterior surface of the base of metacarpal II. Innervation is by the deep branch of the radial nerve adjacent to the elbow.

The insertional tendon of extensor carpi radialis longus courses along the anterior edge of the radius, and is separable only with great difficulty from the adjacent tendon of extensor carpi radialis brevis. Both tendons are crossed by the abductor pollicis longus tendon on the distal one-third of the radius. The tendon splits distally, just before coursing over the extensor grooves on the distal end of the radius. The tendon of extensor carpi radialis longus passes through the anterior extensor groove of the radius, over the manus and to its insertion. In the carpal region, the tendon is crossed by extensor pollicis brevis.

The extensor carpi radialis brevis arises by tendon, along with the long head, from the caudal surface of the epicondylar ridge. The muscle belly largely lies superficial and dorsal to the belly of the long head, and the tendon of insertion courses alongside and dorsolateral to the tendon of the long head. Over the distal radius, the two tendons diverge: the tendon of extensor carpi radialis brevis courses over the medial extensor groove of the radius, across the carpus, and to the insertion on the dorsum of the trapezium and base of metacarpal III.

Comparative aspects. Studies of other bats show little evidence for variation in the attachments of extensor carpi radialis (Vaughan,

1970b; Vaughan and Bateman, 1970; Altenbach, 1979). The muscles are quite similar in form to the same muscle in Alouatta (Schon, 1968) and in rodents (Klingener, 1964). The two heads of extensor carpi radialis are treated as a single entity by Evans and Christensen (1979) for the domestic dog, although the insertions are similar to those described in other mammals.

Functional aspects. The action of extensor carpi radialis is to extend the wing. When the wing is closed, as during roosting or terrestrial locomotion, digits II through V are held approximately parallel with the radius. During the downstroke, the carpus is extended primarily at the radiocarpal joint. The anatomy of both heads of the extensor carpi radialis permits extension at the radiocarpal joint, slight extension across the carpal joints, and both dorsal extension and adduction of digits I and II. The latter action braces the leading edge of the wing against the force of the airstream. Norberg (1972) described the force-lever system of the extensor carpi radialis longus tendon to demonstrate the action relative to a fulcrum at the base of metacarpal II. The dorsal extension and adduction of metacarpal II, in turn, is linked to digit III by the dactylopatagium minus (the wing membrane between digits II and III) and by a ligament between the phalanx of digit II and the middle phalanx of digit III.

Supinator

The supinator originates by a short tendon on the lateral aspect of the lateral epicondyle. The tendon of origin contains a small sesamoid bone. The fibers insert at an angle on the dorsal surface of the proximal 15 mm of the radius. Innervation is by the deep branch of the radial nerve. The belly of supinator is located lateral to extensor carpi radialis longus and medial to the common digital extensor.

Norberg (1970), Vaughan (1970), and Altenbach (1979) described a small sesamoid bone in the tendon of origin. The sesamoid was also present in the tendon of Artibeus, and serves to increase the lever arm of the muscle across the dorsum of the joint. The supinator is a one-joint muscle. This muscle is a flexor of the elbow because movement of the elbow is limited to flexion and extension (Vaughan, 1970b). In rodents and primates, the muscle is similar to the chiropteran supinator (Woods, 1972). However, in these forms, relatively more movement of the elbow is possible and the muscle functions primarily as a weak supinator of the forearm.

Extensor Pollicis Brevis

Form. The extensor pollicis brevis originates by fibers on the lateral interosseous surface of the proximal ulna, and by fibers arising from the deeper abductor pollicis longus. The muscle belly extends along the proximal 25 mm of the radius. The tendon passes through the proximal and middle extensor retinaculum, and then

cranially across the carpus. Insertion of the tendon is on metacarpal I, and on the base of the first phalanx of digit I. Innervation is by the radial nerve.

Comparative aspects. No substantial variation was observed in other chiropteran species. Woods (1972) argued that no extensor pollicis brevis is found in hystricognathous rodents or in most other mammals. However, in bats, the extensor pollicis brevis and abductor pollicis longus diverge in the middle third of the antebrachium and course separately across the ventral and dorsal surfaces of the carpus respectively.

Functional aspects. The extensor pollicis brevis extends digit I at the carpometacarpal and metacarpophalangeal joints. During slow flight the pollex is flexed to increase the camber of the wing. Position of the pollex is controlled by the relative tension produced in the extensor pollicis brevis and in the pollical part of flexor digitorum profundus. Activity in the extensor pollicis brevis counters the downward force of the airstream upon the leading edge of the wing.

Abductor Pollicis Longus

Form. The abductor pollicis longus originates by fibers on the entire lateral interosseous surface of the ulna and adjacent interosseous surface of the radius. The fibers are arranged in a bipinnate fashion on a central tendon of insertion. Distal to the interosseous membrane, the tendon courses over the cranial surface of

the radius, and across the superficial tendons of the extensor carpi radialis. At the distal articular surface of the radius, the tendon courses through a groove on the lateral side of the pseudostyloid process. In the carpus, the tendon is attached to the ventral surface of the scaphoid, and then continues to the ventral base of metacarpal I. Innervation is by the deep branch of the radial nerve.

Comparative aspects. In most bats studied, the insertion of the abductor pollicis longus is on the scaphoid (Vaughan, 1970b). Although insertion on metacarpal one appears to be the usual condition in mammals, Vaughan believed that a scaphoid attachment in bats provided a mechanical linkage between abductor pollicis longus and the base of metacarpal V. He argued that such a linkage facilitated maintenance of the proper angle of attack in the plagiopatagium during flight. In Desmodus, Altenbach (1979) observed two insertions of the abductor pollicis longus that are similar to my observations in Artibeus: one attachment was on the scaphoid while the second attachment was on the surface of metacarpal one. Although the insertion in Antrozous was normally on the scaphoid, the tendon passed across the scaphoid and inserted directly on the thumb pad in one specimen (Hermanson, 1978). No variation was observed in five specimens of Artibeus.

Functional aspects. The abductor pollicis longus functions to abduct the pollex, and thus provides a mechanism for positioning the

pollex. The flexor digitorum profundus simultaneously provides positional control in the flexion-extension plane. Abduction of the pollex occurs during the stance phase of walking. Fine control of the pollex is also observed during head-up landing maneuvers. The connection between the scaphoid and pisiform does not appear to facilitate abductor pollicis longus control over digit V.

Lateral Digital Extensor

Vaughan (1959, 1970_b) referred to this muscle as the extensor digiti quinti proprius.

Form. The lateral digital extensor arises from an aponeurosis on the lateral epicondyle and by fibers along the dorsal, cranial edge of the ulna. The muscle attachments pass caudal to the center of rotation of the elbow joint. A single tendon arises halfway along the caudal aspect of the forearm and passes deep to the proximal extensor retinaculum. Upon emerging from this sheath, the tendon diverges from the adjacent tendon of the common digital extensor and passes caudal to the carpus and the fifth carpometacarpal joint. Eight to ten mm distal to the joint the tendon fuses with a branch from the insertional tendon of the common digital extensor and courses along the dorsal surface of the metacarpal, proximal and distal phalanges of digit V. Extensor aponeuroses are formed over the two distal joints, similar to those already described for the common digital extensor. Innervation is by the deep branch of the radial nerve.

Comparative aspects. Klingener (1964) assembled comparative evidence that extensor digiti minimi (=lateral digital extensor) represents the lateral (ulnar) side of the primitive deep extensors of the antebrachium. In several rodent families, the insertion of the lateral digital extensor inserts on digits four and five (Howell, 1932; Rinker, 1954; Woods, 1972). A similar insertion was noted in primates (Schon, 1968; Howell and Straus, 1933). Vaughan (1959, 1970b) noted that the lateral digital extensor is absent in Eumops and Hipposideros, and is only present on digit V in Myotis. Altenbach (1979) described essentially the same attachments in Desmodus as I have observed in Artibeus. Norberg (1972) described the insertion of the common digital extensor on digits III, IV, and V in Rousettus. However, I believe she included the lateral digital extensor as part of her common digital extensor. Norberg also discussed and illustrated the tendon of common digital extensor coursing from digit IV to the tendon of the lateral digital extensor. I define the two muscles separately because the tendons have separate bellies and the insertional tendons pass the carpus in a different manner. The tendon of the lateral digital extensor passes through the proximal flexor retinaculum while the tendon of the common digital extensor passes through both the proximal and middle retinacula.

Functional aspects. Vaughan (1959) and Altenbach (1979) agreed that the muscle extends and deflects the fifth digit upward. The passage of the tendon caudal to the fifth carpometacarpal joint serves to abduct digit V, an important function in spreading the chiropatagium during the downstroke.

Common Digital Extensor

Form. The common digital extensor crosses several joints, passing from an origin on the distal humerus to digits III - V. The origin of the common digital extensor is by two heads. The superficial head arises by a broad aponeurosis on the lateral epicondyle of the humerus, immediately lateral to the supinator. The deep head arises from a thin tendon of origin that attaches to a small circumscribed area on the lateral epicondyle. The muscle belly lies superficially along the proximal one-half of the forearm, gradually tapering to a distal tendon. This tendon splits along the distal one-third of the radius into two tendons that pass through the proximal and middle extensor retinacula (Fig. 19). Immediately distal to the middle retinaculum, the lateral tendon turns caudad across the carpus and metacarpal IV, giving off a small tendon to digit V that fuses with the tendon of the lateral digital extensor, 8-10 mm distal to the carpal-metacarpal joint. The main tendon to digit IV passes over the carpometacarpal joint and forms an extensor aponeurosis over the metacarpophalangeal joint: central fibers of the extensor hood insert on the base of the proximal phalanx while lateral fibers continue distally. A second extensor aponeurosis

lies over the interphalangeal joint and the attachments are similar. The medial tendon of insertion of the common digital extensor courses across the dorsal surface of the carpus to insert on digit III in a fashion similar to the tendinous attachments described for digit IV. Innervation is by several branches of the deep branch of the radial nerve. Distally, the deep branch runs along the deep surface of the muscle belly. Topographically, the muscle bellies are superficial to the extensor indicis, extensor pollicis brevis, and abductor pollicis longus. Ulnaris lateralis lies caudal to the common digital extensor.

Comparative aspects. There are usually four tendons of insertion of the extensor digitorum (communis) of man although it is common to find only three tendons, where the tendon located on the ulnar side of the wrist gives off a small branch that fuses with the extensor digiti minimi (=lateral digital extensor) (Hollinshead, 1974). The latter condition is identical to my observations in A. jamaicensis. The common digital extensor commonly inserts on digits II to V by four tendons in rodents (Rinker, 1954; Klingener, 1964; Hill, 1937). Woods (1972) observed a similar pattern of insertion but commented on the variable interconnections present between the four tendons in the carpus. Schon (1968) observed five tendinous insertions: one tendon passed to each digit in Alouatta. The significance of this variation is unclear.

Functional aspects. The function of the common digital extensor in A. jamaicensis is to extend the caudal part of the carpus, digits

III to V, and to extend these digits at the carpometacarpal joints, metacarpophalangeal joints, and interphalangeal joints. These muscles probably are important to extend the digits and thus spread the wing at the beginning of the downstroke, as proposed by Vaughan (1959) and Altenbach (1979). If the common digital extensor is active synchronously with the extensor carpi radialis longus, the leading edge of the wing (digit II) is drawn craniad while the trailing edge (digit V) is elevated and extended, thus spreading the chiroptagium.

Extensor Indicis

Form. The origin of the extensor indicis is by fibers along the craniodorsal surface of the ulna, 6-10 mm distal to the olecranon process, and along the interosseous membrane and caudodorsal surface of the middle third of the radius. The tendon of insertion passes through the proximal and middle extensor retinacula, deep to the compartment containing the tendons of the common digital extensor. Extensor indicis inserts on the extensor process of metacarpal II. The tendon continues along the craniodorsal surface of the metacarpal for about 12 mm. The muscle belly is fused along an intermuscular spetum with the belly of extensor pollicis brevis. Innervation is by the deep branch of the radial nerve.

Comparative aspects. In Desmodus, an extensive insertion was described by Altenbach (1979) to digits I through IV. Vaughan (1970b) however, described a single insertion along the dorsum of digit two on the extensor process on the base of the metacarpal.

In rodents, there is generally a single tendon to digit II (Rinker, 1954; Klingener, 1964), although Woods (1972) noted a collateral tendon coursing from the base of digit II to the terminal phalanx of the pollex. Woods suggested that this collateral tendon represented a vestige of the extensor pollicis brevis, a muscle otherwise absent in these rodents. Both the extensor indicis and extensor pollicis brevis are found in bats, representing the deep layer of extensors on the pollical side of the forearm.

Functional aspects. The function of extensor indicis is to extend the digit II and therefore to spread the chiropatagium for the downstroke phase of flight (Altenbach, 1979). This muscle functions as a synergist with the extensor carpi radialis longus.

Ulnaris Lateralis

The ulnaris lateralis is synonymous with the extensor carpi ulnaris of domestic mammals (Evans and Christensen, 1979) and of earlier bat descriptions (Vaughan, 1959).

Form. Ulnaris lateralis arises from the caudal surface of the proximal 4 mm of the ulna. Fibers are arranged in parallel and converge distally on a thin insertional tendon. The tendon courses through the proximal and middle extensor retinacula, deep to the common digital extensor. After crossing the dorsal surface of the cuneiform, the tendon of ulnaris lateralis inserts in a groove on the craniodorsal base of metacarpal V. Innervation is by the deep branch of the radial nerve.

Comparative aspects. The proximal attachment of the ulnaris lateralis is conservative in all bat species studied. The insertion, however, exhibits variation among several species. In Macrotus and in Desmodus the ulnaris lateralis inserts upon the base of metacarpal five (Vaughan, 1959; Altenbach, 1979). In Antrozous, Plecotus, Myotis, and Eumops the muscle inserts upon the dorsal surface of the base of metacarpal three. The attachments are similar in other mammals. The common position of insertion of ulnaris lateralis in rodents is on metacarpal V (Woods, 1972).

Functional aspects. The insertional tendon of ulnaris lateralis approaches the base of metacarpal V along a vector caudal to the radiocarpal joint and the carpometacarpal joint of the digit V. Thus, tension in the muscle will flex metacarpal V upon the radius. Ulnaris lateralis is the only muscle of the antebrachium, innervated by the radial nerve, to perform a flexor function. Vaughan (1959) and Norberg (1970) claimed that the extensor carpi ulnaris was an extensor of the metacarpal V in Macrotus and Plecotus, respectively. They did not, however, provide a mechanical explanation for their observations. The tendon of insertion courses sufficiently caudal to the carpus to effect a weak flexion of the metacarpal. Because the wing membrane connects the four lateral digits, flexion of digits II through IV will also result when digit V is flexed. Flexion of the wing occurs during terrestrial locomotion and roosting, and transiently during the upstroke of flight.

Antebrachial Flexor Group

Flexor Carpi Radialis

Form. This muscle originates by fibrous attachments along the medial surface of the proximal radius, and by fibers arising from the surface of the pronator teres, exclusive of the proximal 8 mm of the latter muscle. Flexor carpi radialis inserts by a thin tendon on the ventral base of metacarpal II. The muscle is pinnate: the belly extends about 20 mm distal to the elbow joint. Innervation is by the median nerve.

Comparative aspects. The muscle is well developed in Macrotes but is vestigial in Eumops and Myotis (Vaughan, 1959). In Macrotes, the muscle inserts on the base of metacarpal III. The attachment of the insertional tendon is on the base of metacarpal II in Rousettus (Norberg, 1972) and Desmodus (Altenbach, 1979).

Functional aspects. Vaughan (1959) believed that the insertion of flexor carpi radialis on metacarpal III provides the mechanical arrangement necessary to flex the chiropatagium. Because of the attachment of the wing membrane between the digits, flexion of metacarpal III would synchronously flex metacarpal II, the leading edge of the wing. Similarly, flexion of the chiropatagium would be achieved by the flexion of digits III through V by the flexor digitorum profundus. The direct attachment of flexor carpi radialis on digit II could provide additional control of the leading edge of the wing as well as control over the folding of the wing that is necessary during terrestrial walking behavior (Altenbach, 1979).

Figure 20.--Medial view of muscles of the elbow region. The superficial layer of muscles is exposed.

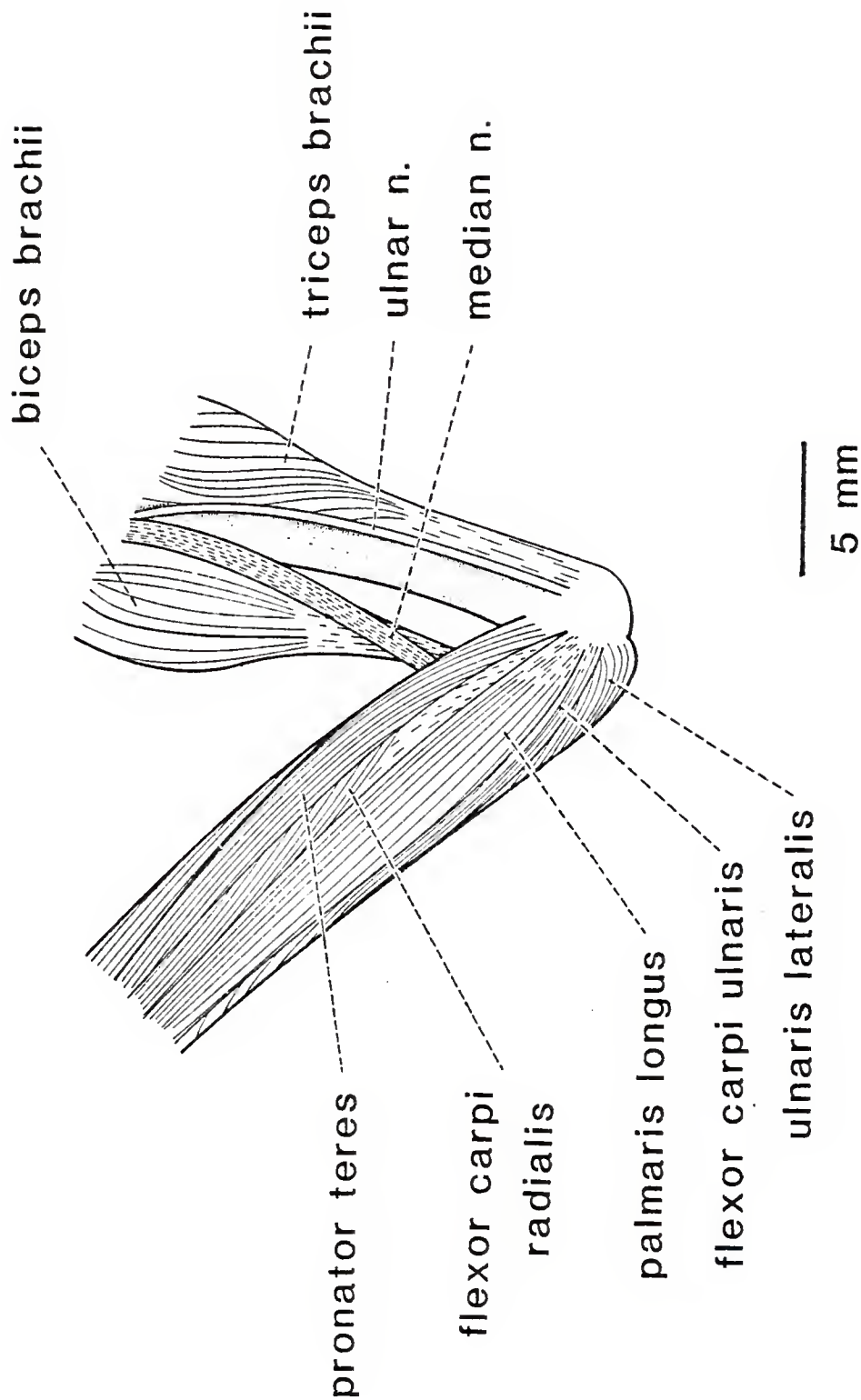
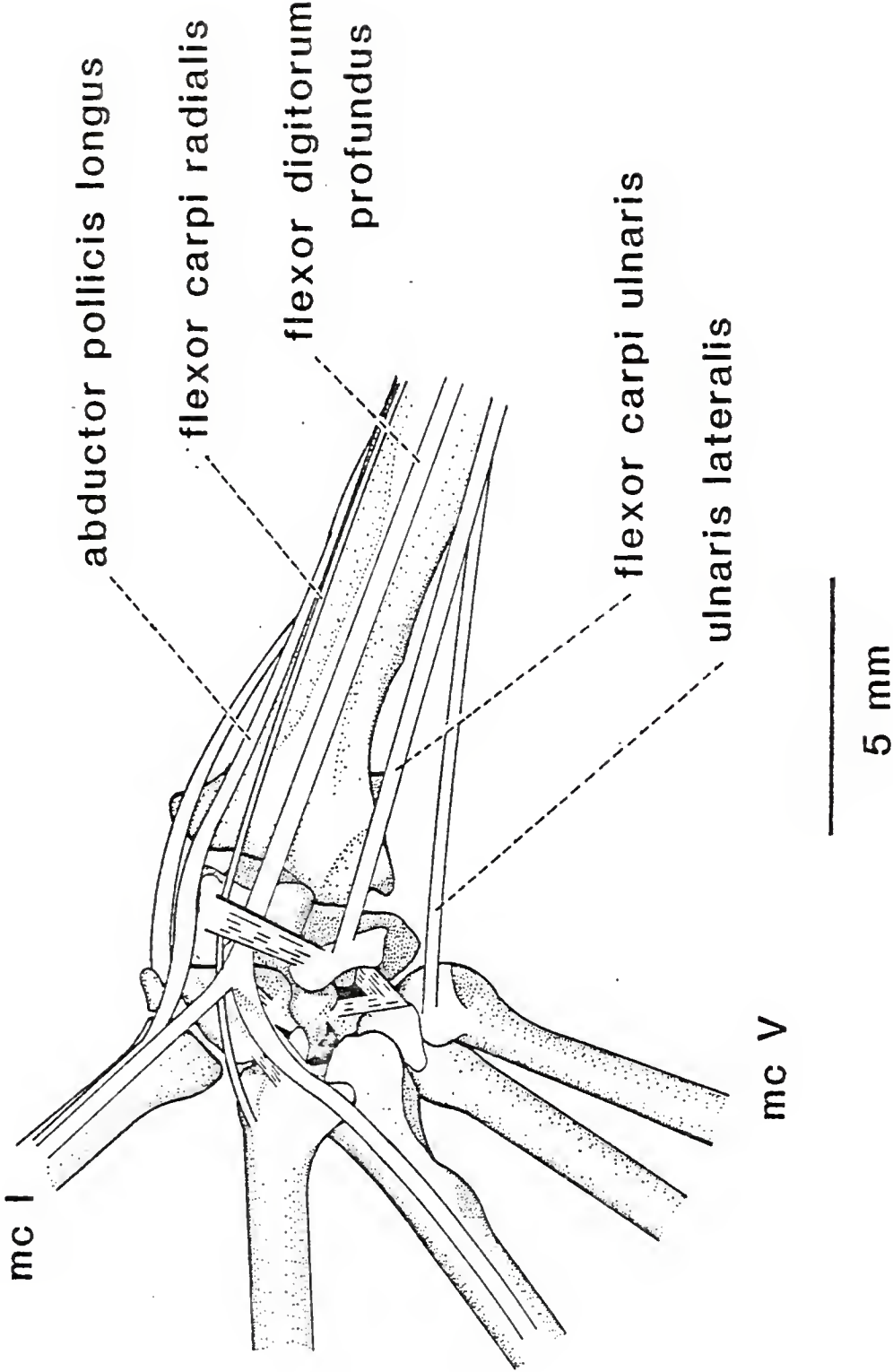


Figure 21.---Ventral view of the muscles of the carpal region. The intrinsic muscles of the manus have been removed.



The latter function may not be a specialized role or indication of advanced structure. Attachment of the flexor carpi radialis on digits II and III is common in many mammals (Woods, 1972).

Pronator Teres

Form. Pronator teres originates by a tendinous attachment on the proximal aspect of the spinous process of the humerus. Insertion of the muscle is by fibrous attachments along the ventral surface of the radius, extending 24 mm distal from the elbow joint. Innervation is by the median nerve.

Comparative aspects. The attachments of this muscle are similar in all bats (Vaughan, 1959, 1970b). The muscle is only a weak stabilizer of the elbow because of the limited pronation and supination possible at this joint.

Functional aspects. The muscle is primarily a ventral stabilizer of the humeroradial articulation. Some pronation of the radius is possible because of the potential for rotatory movements of the radial head on the capitulum of the humerus. In bats with elbow movement restricted to flexion or extension, the pronator teres is relatively small (Vaughan, 1959).

Palmaris Longus

Form. The origin of the palmaris longus is by a short tendon to the spinous process of the humerus, and by fibers from the caudal surface of a broad sheet of connective tissue on the proximal flexor carpi radialis. The belly of palmaris longus extends 26-30 mm along the radius. The insertional tendon bifurcates over the carpus. The medial tendon courses to the ventral base of the metacarpal I.

The lateral tendon passes lateral to and inserts on the lateral aspect of metacarpal I. Innervation is by the median nerve.

Comparative aspects. The palmaris longus has been described in all bats studied except Myotis (Vaughan, 1959, 1970a). In Eumops, the muscle inserts on the deep palmar fascia, on the thumb pad, and on the surface of the abductor digiti quinti (Vaughan, 1959). Extensive insertions were also described in Rousettus (Norberg, 1972), Plecotus (Norberg, 1970), and Desmodus (Altenbach, 1979). In these bats, the palmaris longus attached upon digits I, II, III, and V.

Functional aspects. The palmaris longus of Artibeus contributes to flexion of the digit I along with the flexor digitorum profundus. Ventral flexion of the pollex during slow flight increases the camber of the middle wing sections and increases lift. This function is most apparent in Artibeus, a bat that often flies slowly while carrying large weight.

Flexor Carpi Ulnaris

Form. The flexor carpi ulnaris originates by two heads: one head arises from a tendinous attachment on the distal tip of the spinous process of the humerus, distal to the origin of the flexor digitorum profundus and palmaris longus: a few fibers arise from the proximal 8 mm of the ventral surface of the ulna. The two heads fuse along the proximal third of the radius and the common belly extends about 20 mm distal to the elbow joint. The muscle inserts by

a tendon on the palmar surface of the pisiform. Innervation of both heads is by the ulnar nerve.

Comparative aspects. The attachments of this muscle are similar in all species studied. Variation is observed primarily at the proximal end of the muscle. The origin of flexor carpi ulnaris in Macrotus includes attachments to both the radius and ulna (Vaughan, 1959). In Desmodus, the muscle originates from the ulna and the surface of palmaris longus (Altenbach, 1979). Attachments of muscle in Rousettus (Norberg, 1972) are identical to those of Artibeus.

Bats that are highly specialized for high-speed flight, such as the molossids, usually possess a long projection on the distal aspect of the spinous process. This bony modification, along with reduction in the mass of muscle fibers inserting on the tendon of flexor carpi ulnaris, permit an automatic mechanism for flexion of the manus when the elbow is flexed during flight or roosting (Vaughan, 1959, 1966).

Variation in the origin of the flexor carpi radialis is common in rodents (Woods, 1972). The primitive condition in mammals is for the muscle to originate from the medial epicondyle, (Hill, 1937).

Functional aspects. On the basis of size and mechanical advantage, I conclude that flexor carpi ulnaris is the major flexor of the chiropatagium. The insertion of the flexor carpi ulnaris is on the pisiform, a bone firmly bound to the adjacent carpal bones and to the proximal base of metacarpals IV and V. Tension exerted upon the pisiform is transmitted indirectly to the metacarpals and

folds the wing during roosting, walking, or during the middle portions of the upstroke. The muscle probably acts synergistically with the ulnaris lateralis.

Flexor Digitorum Profundus

Form. This deep digital flexor muscle originates by three heads. The humeral head takes origin by a thin tendon from the medial epicondyle between the origins of pronator teres and flexor carpi ulnaris, and by tendinous slips from the deep surface of the tendon of palmaris longus. The fibers are arranged in parallel. The radial head arises by fibers along the ventral surface of the proximal 22 mm of the radius. The fibers are unipinnate. The ulnar head arises by fibers along the proximal 24 mm of the ventral surface of the ulna. The fibers are unipinnate in their attachment upon the main tendon of insertion. The three heads fuse along the proximal third of the radius. The tendon passes deeply through the flexor retinaculum of the carpus before bifurcating. One branch of the insertional tendon attaches on the bases of phalanges I and II of the pollex. The second tendon attaches on the ventromedial base of the second phalanx of digit III. Innervation of the three heads of flexor digitorum profundus is by the median nerve.

Comparative aspects. The flexor digitorum profundus of bats has a reduced insertion on the digits relative to terrestrial mammals. In many rodents, the muscle inserts by four heads on digits II through V (Klingener, 1964; Woods, 1972). Innervation of the muscle is by branches of the median nerve to all heads in cricetine (Rinker,

1954) and dipodoid rodents (Klingener, 1964). In hystricognathous rodents, however, the ulnar head of flexor digitorum profundus is innervated by the ulnar nerve while the remaining heads are innervated by the median nerve (Woods, 1972). The innervation of all three heads is derived from the median nerve in bats (Vaughan, 1959). The only branches of the ulnar nerve that I observed in the proximal antebrachium in Artibeus provide motor innervation to the flexor carpi ulnaris.

In other bats, the insertion of flexor digitorum profundus is on digits I and III in Desmodus (Altenbach, 1979) and Macrotus (Vaughan, 1959). In Myotis, the insertion is on digits I, III, and IV; and in Eumops the insertion is on digits I and V (Vaughan, 1959).

Rousettus, a megachiropteran, exhibits an insertion of the muscle on digits I, II, and III (Norberg, 1972).

Functional aspects. Insertion on digit III provides a direct line of pull for this muscle to flex the digit upon the radius and thus fold the wing during roosting or terrestrial locomotion (Altenbach, 1979). During the downstroke, flexion of the digit III is important to prevent dorsiflexion of the digit and loss of wing camber. Additionally, flexion of the chiropatagium during the late upstroke reduces the amount of drag on the wing as it is returned to a dorsal position for the ensuing downstroke.

ELECTROMYOGRAPHY IN FLYING BATS

Electromyographic data for 17 shoulder and arm muscles in Antrozous indicated that muscles could be characterized as adductors, abductors, or bifunctional muscles (Hermanson and Altenbach, 1983). This classification paralleled the flexor, extensor, and bifunctional categories proposed for terrestrial mammals by Engberg and Lundberg (1969). Electromyographic data obtained in the present study do not present such a clear functional classification for 15 of these muscles. Data are not available for two muscles in Artibeus, the long and short heads of biceps brachii. In Artibeus, two phases of activity are demonstrated in 10 muscles, eight of which were uniphasic in Antrozous (Hermanson and Altenbach, 1983). In this chapter, differences in the pattern of muscle activity between Antrozous and Artibeus are discussed, and data for both species are compared with similar studies of locomotion conducted on terrestrial mammals.

There are several differences in the abductor muscle category between Artibeus and Antrozous. In Artibeus, these muscles include the clavotrapezius, acromiotrapezius, latissimus dorsi, teres major, acromiodeltoideus, spinodeltoideus, and two heads of triceps brachii. Two muscles are added to and one subtracted from the abductor category in Antrozous (Hermanson and Altenbach, 1983). All of the abductors

except triceps brachii of Artibeus exhibit two periods of activity. A primary EMG burst corresponds with the transitional period between the downstroke and upstroke and is similar in timing to EMG activity reported for abductors in Antrozous. In the biphasic abductors, a secondary EMG burst, characterized by low-amplitude electromyograms, occurred during the late upstroke and early downstroke, a period appropriate for adductor function.

Latissimus dorsi and teres major both exhibit biphasic activity cycles and are classified as abductors. Both exhibit single-phase activity cycles in Antrozous and were classified as an adductor and a bifunctional muscle, respectively (Hermanson and Altenbach, 1983). In Artibeus, a high-amplitude burst of activity in these muscles precedes the beginning of the upstroke and coincides with the primary activity of the other abductors. A synergistic function appears to exist between these two muscles based upon their common insertion and similar EMG profiles. Both contribute to arrest the cranial sweep of the wing during the late downstroke and to power abduction of the wing during the upstroke. The second burst of activity, immediately before and during the early downstroke, provides the pronator action necessary to position the wing for the downstroke. Similar to a mechanism proposed in Desmodus, the combined action of latissimus dorsi and teres major of Artibeus powers the flick phase, during which the wingtip is rapidly pronated so that the leading edge of the wing faces ventrally.

The triceps brachii, long and lateral heads, exhibit uniphasic EMG patterns in Artibeus. The activity of triceps brachii in Antrozous is similar (Hermanson and Altenbach, 1983). In both species, the long head commences activity prior to and continues for a longer duration than the lateral head. Flexion of the elbow through the first two-thirds of the upstroke was demonstrated in Plecotus by Norberg (1976). A similar pattern of joint movement is present in Artibeus. Thus, it is an enigma that triceps brachii is active primarily as an abductor during a period of the wingbeat when the elbow is rapidly flexed.

Spinotrapezius and infrapinatus both exhibit two periods of activity in Artibeus. For both muscles, each period exhibits electromyograms of approximately the same amplitude, thus it is difficult to describe either as primary or secondary. I classify both as bifunctional. Spinotrapezius is situated on the dorsum and is in a position to draw the caudal angle of the scapula caudally and medially. In Antrozous, spinotrapezius was uniphasically active and was characterized as an abductor. Infrapinatus is located on the infrapinous fossa and is situated to supinate the humerus and flex the shoulder. Electromyograms in Antrozous were biphasic, indicating activity during both the adductor and abductor periods (Hermanson and Altenbach, 1983). Electromyography in Artibeus suggests that both spinotrapezius and infrapinatus serve to abduct the wing during the early upstroke. Coactivation of spinotrapezius and infrapinatus

with adductor muscles indicates that the interplay between these muscle groups serves to smooth the transition from upstroke to downstroke, and therefore protect the shoulder joint from disarticulation resulting from the powerful activity of the adductors and the sudden forces imparted to the wing when it first meets resistance from the airstream.

Three adductor muscles were identified in Antrozous, including pectoralis, serratus ventralis thoracis, clavodeltoideus, and latissimus dorsi (Hermanson and Altenbach, 1983). In Artibeus, only three adductors are noted: clavodeltoideus, serratus ventralis thoracis, and pectoralis. The activity of these three muscles is similar to that observed in Antrozous except for the addition of a low-amplitude period of activity in clavodeltoideus and serratus. Pectoralis commences adductor activity slightly before serratus (0.781 versus 0.823) and both terminate activity during the early to middle downstroke. The secondary burst of EMG activity in clavodeltoideus and serratus occurs during the early upstroke, a period appropriate for abductor activity. This secondary activity in both muscles probably stabilizes the scapula against the forces developed by the primary activity of the acromiotrapezius and clavotrapezius. Clavodeltoideus, serratus, and subscapularis are the only ventrally situated muscles active during the early upstroke.

Six muscles were studied in Artibeus that were classified as bifunctional muscles in Antrozous (Hermanson and Altenbach, 1983).

They included both heads of biceps brachii, supraspinatus, infraspinatus, teres major, and subscapularis. No EMG data are available for the biceps brachii of Artibeus. The spinotrapezius represents an addition to the list of bifunctional muscles in Artibeus. The spinotrapezius and infraspinatus of Artibeus exemplify the bifunctional pattern. Activity is concentrated around the two transition points of the wingbeat, the beginning of both the downstroke and the upstroke. High-amplitude activity occurred during both of these periods. The pattern in Antrozous was different for spinotrapezius but was similar for infraspinatus (Hermanson and Altenbach, 1983). Supraspinatus, a part of the rotator cuff complex and a muscle that is situated in approximation with the infraspinatus exhibits a different pattern of activity than was observed in Antrozous. In Antrozous, two bursts of activity were confined to the early upstroke phase (Hermanson and Altenbach, 1983). In Artibeus, however, a single burst of activity begins during the middle upstroke and continues throughout the early downstroke. The small sample size (N=6) and the interruption in EMG activity observed during the burst in two wingbeats suggest that the general pattern of activity in Artibeus may not be significantly different from Antrozous. On the basis of observed EMG activity, the spinotrapezius, infraspinatus, and supraspinatus are active slightly before the major adductors, the pectoralis and serratus ventralis thoracis. Their function is to stabilize the shoulder joint and scapula against the larger forces produced by these adductors.

Subscapularis is a difficult muscle to classify. In mammals, the muscle forms the ventral component of the "rotator cuff," stabilizing the shoulder joint and effecting pronation of the humerus (Hollinshead, 1974; Tuttle and Basmajian, 1978). In bats, however, the subscapularis attains the largest size relative to body mass observed in the class Mammalia (Vaughan, 1959), an observation that led Vaughan to conclude that the subscapularis functioned as a critical member of the downstroke musculature as well as a shoulder stabilizer. In Antrozous, subscapularis was found to be active throughout most of the wingbeat cycle (Hermanson and Altenbach, 1981). A second study led these authors to note a biphasic distribution of activity frequency. However, Hermanson and Altenbach concluded that the muscle was essentially active throughout the wingbeat cycle, as demonstrated by the large variation in onset and termination times (Hermanson and Altenbach, 1983). The muscle is not primarily an adductor, but stabilizes the shoulder joint and provides for fine control of humeral movements. The variation observed in level flight reflected the facultative role of this muscle in the control of flight. In Artibeus, subscapularis is active throughout the wingbeat cycle, and is quiescent only during the third-quarter of the downstroke. This is similar to data presented for Antrozous. High-amplitude activity occurred during the last-third of the upstroke and during the early downstroke. This high-amplitude activity must contribute to the downstroke by pronating the wing and maintaining the ventral orientation of the wing's leading edge during the downstroke.

Different flight styles and wing shapes of Artibeus and Antrozous may require differences in the basic neuromuscular program for flight. Artibeus is a heavier bat than Antrozous. I converted Davis's data (1969) for wing loading in Antrozous into M-K-S system equivalents. The mean wing loading in Antrozous was 12.67 N/m^2 , a value that includes males and females throughout the annual cycle. Fall females were found to exhibit relatively heavier wing loading values than pregnant females or adult males. Estimates of wing loading in Artibeus range from 16.60 N/m^2 to 16.65 N/m^2 (Norberg, 1981). My observations of wing loading values in two Artibeus females, 15.47 and 16.74 N/m^2 , represent extremes relative to these published accounts. A range of males and females from different seasons is not available. The wing loading values of Artibeus are larger than observed in Antrozous, and indicates that the wing supports more weight per square meter of wing surface. Additional muscular effort in the form of secondary bursts of muscle activity, are necessary to control wing position and shape with precision during the wingbeat of Artibeus. One difference is the addition of a second phase of activity in eight muscles of Artibeus that were uniphasic in Antrozous. The turnover points of the wingbeat, at the end of the downstroke or upstroke, are smoothed out by coactivation of abductors and adductors. Analysis of the EMG profiles shows that the additional burst of activity found in

the eight additional biphasic muscles generally occur either at the end of the downstroke or at the end of the upstroke. Because of the elliptical path followed by the wingtip during the wingbeat cycle, the transitions between the propulsive and non-propulsive phases are not as clearly defined as they are in terrestrial stepping movements.

In review, a classification of the 15 muscles studied in Artibeus includes eight abductors, three adductors, and four bifunctional muscles. Four of the muscles are classified differently than they were in Antrozous.

The classification of muscles as adductors, abductors, and bifunctional muscles is an heuristic tool to analyze the contribution of each group of muscles to the overall control of the wingbeat cycle. The following discussion identifies the muscles, or muscle group, that power specific portions of the wingbeat cycle.

The downstroke phase is preceded by increasing amounts of activity in the adductor muscles. All three adductor muscles are active before the end of the preceding wingbeat (by the .850 point). The adductors remain active during the first one-fifth of the downstroke. Five of the abductor muscles are active during the last one-fifth of the upstroke or by the .900 point of the wingbeat cycle. Six abductor muscles are active at the beginning of the downstroke (.000-.005). Abductor activity decreases rapidly during the early downstroke and, at .100, only two muscles, acromiodeltoideus (caudal part) and

spinodeltoideus are active. In all cases, the electromyograms of the abductors during the upstroke to downstroke transition are of lower amplitude than observed during activity associated with the end of the downstroke. The spinotrapezius has a temporal pattern of activity that is similar to the abductors, however, the electromyogram obtained at the upstroke to downstroke transition is equal to the second burst observed during the late downstroke. Therefore, spinotrapezius is classified as a bifunctional muscle. Three additional bifunctional muscles are active prior to and at the beginning of the downstroke: they include the supraspinatus, infraspinatus, and subscapularis. Spinotrapezius, supraspinatus, and infraspinatus are all situated on the dorsal aspect of the shoulder girdle and should cause abduction of the wing when active. Their contribution to the downstroke is apparently one of joint stabilization. Subscapularis is situated ventral to the shoulder joint and was proposed to be a major adductor muscle (Vaughan, 1959). During the early downstroke, subscapularis probably contributes to power the adduction of the wing.

The primary downstroke muscles in Artibeus include pectoralis, serratus ventralis thoracis ventralis (caudal division), and clavodeltoideus. These muscles cease activity early during the downstroke and are quiescent during about four-fifths of the downstroke. This absence of activity cannot be explained without undertaking mechanical studies of the muscles. Rasmussen et al. (1978) commented on the termination of EMG activity in all extensors of the

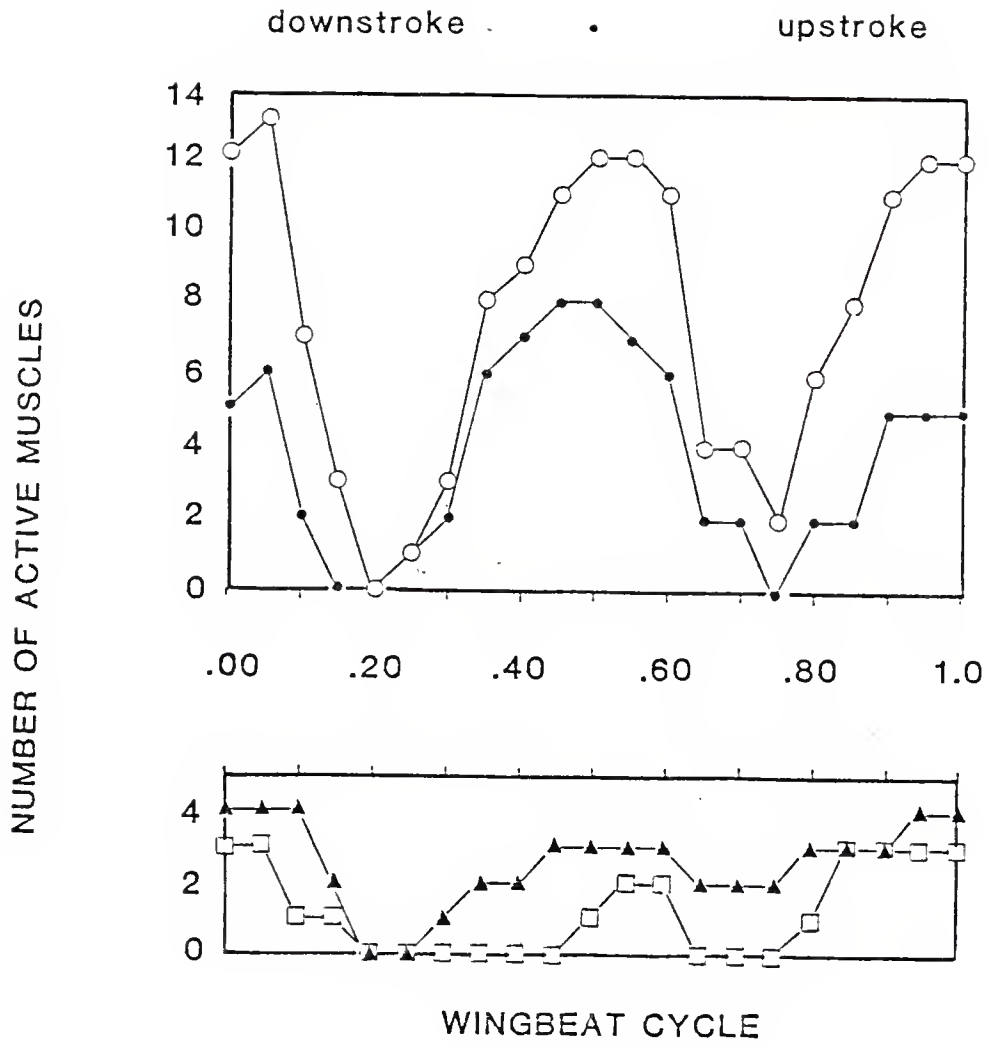
cat hindlimb prior to the end of the extensor phase (E3) during normal stepping. These authors attributed the early termination of activity to "unloading" of the limb, a relaxation of all extensor muscles, before the subsequent flexion period begins. In Artibeus, no EMG activity was recorded from abductors or adductors during the second-quarter of the downstroke (.270-.470), except for the final myopotentials observed in infraspinatus (until .120) and subscapularis (until .174). The termination of adductor muscle activity some 30-40 msec prior to reversal of the wingbeat is puzzling and needs further analysis.

The initiation of upstroke movements is characterized by increasing activity in the abductor muscle group. Beginning with a minimum of no muscle activity during the mid-downstroke, the .200 point of the wingbeat cycle, the total number of abductor muscles showing activity increases to seven by the last one-fifth of the downstroke (the .400 point), and to a maximum of eight muscles by the time the first upward movements of the wingtip are noted. The number of coactive abductors decreases during the early upstroke, decreasing to six muscles by the .600 point, and to two muscles at the .650 point. Thus, the primary coactivation of abductor muscles occurs for about 15 msec before and 10 msec after the beginning of an upstroke. Two adductor muscles are coactive with the abductors during the early upstroke: the serratus ventralis throacis and the clavodeltoideus. This coactivation of antagonists parallels the situation observed during the transition between the downstroke and upstroke.

The most prominent pattern of muscular coactivation during the chiropteran wingbeat cycle is the concentration of muscles, in absolute numbers, that are active at the transitional points of the cycle. In Artibeus, the maximal number of coactive muscles observed, 13, occurs at the beginning of the downstroke (Figure 22). The frequency or number of coactive muscles has a bimodal distribution, one peak being at the beginning of the downstroke, the other at the beginning of the upstroke when 12 muscles are coactive. Other intervals show decreasing numbers of coactive muscles with none acting during the middle of the downstroke, and a second minimum of two muscles during the upstroke. Electromyograms of Antrozous during flight indicate a similar emphasis of muscle activity around the transitional points of the wingbeat cycle. The absolute number of coactive muscles is less than that observed in Artibeus because the abductors do not develop secondary periods of myopotentials (Hermanson and Altenbach, 1983).

The mode of support and propulsion in bats can be compared aptly with those in terrestrial mammals. In terrestrial locomotion, several muscles transmit the body weight to the limbs and therefore hold the body off of the ground. Comparative anatomists recognized that the serratus ventralis was ideally situated to function as a "sling" to suspend the thorax between the forelimbs (Davis, 1949; Gray, 1968). This "sling" hypothesis has been confirmed by electromyographical studies which reveal intense activity of several regions of the serratus ventralis thoracis during the stance phase in stepping

Figure 22.--Number of coactive muscles during the wingbeat cycle: all muscles studied (o); abductors (); adductors (); bifunctionals ().



cats (English, 1978a) and opossums (Jenkins and Weijs, 1979). Jenkins and Weijs (1979) suggested that the pectoralis transversalis and rhomboideus also function to suspend the body between the forelimbs.

Flying mammals contend with similar problems during the propulsive phase as the body must be supported between the two wings. Serratus ventralis thoracis (caudal division), pectoralis and spinotrapezius are all extrinsic muscles transmitting weight from the wing to the thorax and are intensely active during the downstroke. Clavotrapezius and acromiotrapezius also show activity, albeit low-amplitude activity, during the propulsive or downstroke phase. All of these muscles appear to transmit the weight of the body to the wings, or to stabilize rotatory movements of the scapula along its long axis. No EMG data is available for rhomboideus, however, in bats the rhomobuideus is a thin sheet and may not be of great importance. Clavotrapezius and acromiotrapezius are thick muscles and are ideally suited by virtue of their origin from the cervical vertebrae, 10-15 mm ventral to the scapula to support the body between the forelimbs.

The intrinsic muscles of the shoulder include the supraspinatus, infraspinatus, and subscapularis. Each of these crosses one joint, the shoulder joint, and exhibit activity in bats during the transitional periods between the upstroke and downstroke. The shallow profile of the glenoid fossa provides poor stability for the shoulder joint except for stability provided by the rotator cuff muscles. Compression of the

suprascapular nerve in horses, the sole motor nerve supply to both the supraspinatus and infraspinatus, two of the four rotator cuff muscles, results in subluxation of the joint during the stance phase of stepping or during quiet standing (Rooney, 1969; Adams, 1974). In the opossum, stability of the shoulder joint was provided by the almost synchronous activity of supraspinatus, infraspinatus, and subscapularis during the last half of the swing phase and throughout most of the propulsive phase (Jenkins and Weijs, 1979). These muscles were active during the E1 through E3 phases of the step cycle in cats (English, 1978a). In both cases, activity during the E1 phase, or the first extension phase prior to foot touchdown, indicates that the rotator cuff muscles are also important in positioning the limb for the ensuing step.

Propulsion of the body is realized in a different fashion in bats and in terrestrial mammals. During terrestrial locomotion, the body is propelled forward through the forelimbs by action in two muscles, caudal portions of latissimus dorsi and pectoralis (Tokuriki, 1973a; Jenkins and Weijs, 1979; English 1978a). Kinematic analysis indicated that the greatest contribution to propulsion is incurred by the proximal part of the limb: movements of the scapula relative to the thorax are of greater magnitude than are synchronous joint angle changes in the elbow and carpal joints (Jenkins and Weijs, 1979). Activity of the intrinsic limb musculature, therefore, contribute to stabilization of the limb in order that the trunk musculature (i.e., latissimus dorsi and pectoralis) causes the body to pole vault

over the limb. Additionally, the pectoral limbs are thought to serve primarily as weight-bearing organs while the pelvic limb provides most of the forward thrust associated with locomotion in mammals (Manter, 1938). In bats the pectoral limbs provide both weight support and propulsive forces. During the downstroke, the wing moves ventrally and cranially. Because of its dorsal point of origin, the latissimus dorsi lengthens during the propulsive phase, the downstroke. In Artibeus, latissimus dorsi is classified primarily as an abductor. The muscle is intensely active during the upstroke, and active as a wing pronator during the downstroke. Thus, latissimus dorsi has a different role in flying bats than is commonly required during stepping in mammals.

Vaughan (1959) and Altenbach (1979) noted the significance of a relatively large latissimus dorsi in bats that spend large amounts of time foraging on the ground. It would not be surprising to observe primary propulsive activity in the latissimus dorsi during walking in bats if EMG studies are conducted. The pectoralis is active as an adductor in Artibeus. Because of the ventral origin of this muscle, the muscle is ideally situated as a wing adductor. Shortening of the muscle during the wingbeat may amount to only 10 percent of the muscle's maximum length, permitting the muscle to operate within a range of high efficiency of force production (Hermanson, 1981). Pectoralis exhibits temporal patterns of activity that are similar to those observed in terrestrial mammals.

CONCLUSIONS

Comparison of the activity patterns of homologous flight muscles in two distantly related bats Artibeus jamaicensis and Antrozous pallidus, indicates divergent activity correlated with their different flight characteristics. These bat species are similar in the gross appearance of skeletal and muscular systems despite their divergent familial affinities. Their flight styles reflect adaptation to their respective feeding behaviors. Artibeus is frugivorous and flies directly to and from food sources at low to medium speed while moving over short distances. The relatively heavy wing loading values observed in Artibeus compromise their maneuverability. In contrast, Antrozous feeds upon insects in aerial, arboreal, and terrestrial niches. They are capable of slow, fluttering flight while foraging but can travel long distances nightly during flights of three or four hours. The temporal patterns of muscle activity recorded during EMG experiments on the two species differ, just as do their flight styles. These data, interpreted in light of the differences noted in the flight style of both species, suggest the use of caution in speculation about the neuromuscular control of flight in other bats that utilize divergent or similar flight styles.

Electromyograms obtained from eight of the 15 muscles studied in Artibeus exhibited a biphasic pattern not recorded in the same muscles in Antrozous. These observations of biphasic muscles could relate to increased stabilization roles encountered in Artibeus. I argued (see preceding chapter) that the heavier wing loading of Artibeus, relative to Antrozous, necessitates increased muscle activity at the turnover points of the wingbeat cycle. This additional activity maintains a smooth transition in changing the direction of wing movements. Most of the muscles in Artibeus exhibited a high-amplitude period of activity that is similar in timing to the single phase of activity that was identified in the same muscles of Antrozous. Electromyographic studies on other chiropteran species that are specialized for different flight styles or that exhibit skeletal specializations may provide data useful in evaluating these ideas.

Morphological studies conducted on locomotion in several terrestrial mammals emphasize the facultative nature of stepping (cf. Rasmussen et al., 1978). The variation in the neuromuscular control of bat flight is also demonstrated by the data presented for the individual muscles of Artibeus. It is possible to compare homologous muscles in the wings of flying bats and to the limbs of other mammals while stepping with the aid of the statistical means of activity onset and termination. For example, bats support the body in a fashion similar to terrestrial mammals: the body is supported between the two pectoral limbs by the serratus ventralis thoracis

muscles, and partly by the pectoralis and trapezius muscles. The recruitment of muscles during the propulsive phase of the locomotor cycle is different in the two groups, however. In bats, the propulsive or downstroke phase is powered primarily by the pectoralis and serratus ventralis thoracis musculature. In cats and dogs, propulsion is largely realized when the latissimus dorsi and caudal portions of the pectoralis pull the body cranially relative to the fixed pectoral limbs. Also, the activity cycle of the propulsive muscles is more rapid in bats than in most terrestrial mammals. Correlation of these functional data with further studies on the physiological specializations of bat muscles will yield insights into the range of functions possible for mammalian muscle tissue.

The pattern of muscle recruitment and activity in Antrozous is simple relative to the complex pattern observed in many of the muscles of Artibeus. The flight muscles of Antrozous can be classified as abductors, adductors, or bifunctionals, a scheme that parallels the extensor, flexor, or bifunctional classification proposed for locomotory muscles in cats during overground stepping. The dichotomy between abductors and bifunctionals is not clear in Artibeus EMG recordings where the biphasic patterns are most common. A correlation exists between the complexity of the muscle activity patterns and musculoskeletal structure. Antrozous is a typical vespertilionid bat and possesses a well developed shoulder locking mechanism. This

locking mechanism provides a skeletal constraint on wing movement. Vespertilionids are derived chiropterans and are specialized for flight. In contrast, Artibeus is a typical phyllostomid and possesses a poorly developed shoulder locking mechanism. Phyllostomids are more primitive chiropterans and exhibit generalized flight characteristics. The more complex activity patterns of Artibeus, relative to Antrozous, reflect the need for more gross muscular control of the wingbeat cycle, particularly during the transition between the upstroke and downstroke.

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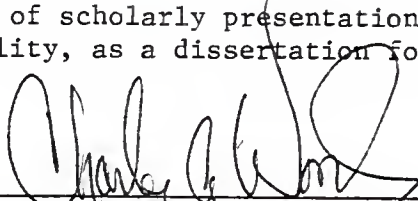
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BIOGRAPHICAL SKETCH

John W. Hermanson was born in Quincy, Massachusetts, the son of John and Mary Hermanson. He attended the University of Massachusetts, at Amherst, and received the degree of Bachelor of Science in Zoology in 1975. He studied in the Department of Biological Sciences at Northern Arizona from August 1975 through August 1977. The degree of Master of Science was awarded to him in 1978 after completion of his thesis, "The forelimb morphology of the pallid bat (Antrozous pallidus)."

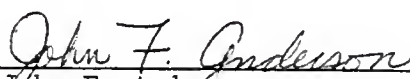
In September 1977, he entered the graduate program at the University of Vermont to study with Dr. Charles Woods. He went with Dr. Woods to the University of Florida in 1980 and enrolled there as a graduate student in the Department of Zoology. During his tenure at the University of Florida, his primary duties were as a graduate teaching assistant in Anatomy in the College of Veterinary Medicine.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



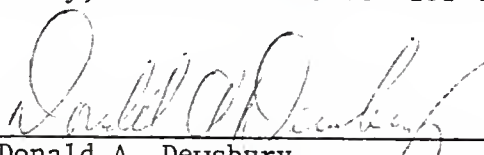
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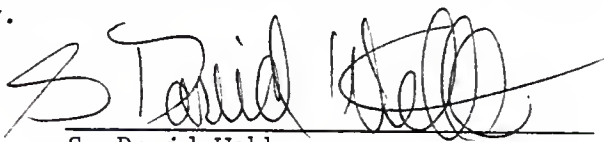
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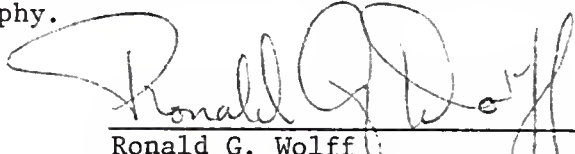
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Professor in Zoology

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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